





# HUMAN BIOLOGY

a record of research

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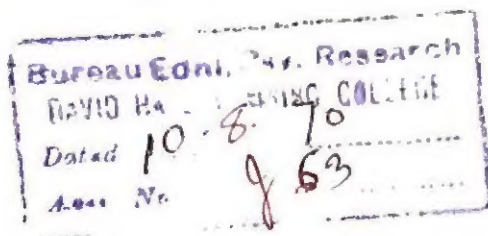
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# HUMAN BIOLOGY

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## FORENSIC ANTHROPOLOGY IN GERMANY

BY ILSE SCHWIDETZKY

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IN January, 1953, while the author was awaiting her visa in the U. S. Consulate at Frankfurt, she read in an American magazine a story concerning the daughter of a Mrs. M. from Chicago who had been kidnapped when she was two years old. Since that time she had been sought by her mother. Twenty-two years later, through the help of some newspapers, a young woman was found in California who might possibly be the lost child. She was brought to Chicago, and two photographs show how the head and face of the mother and the presumptive daughter were measured. However, only a few newsmen were impressed by such methods. The young woman returned to California, and Mrs. M. shut the door finally to reporters.

In Germany, a number of such cases have been worked on by anthropologists and human geneticists in recent years. Many families were separated at the end of the war by the Soviet invasion, by the flight of the population from Eastern Germany, and by the disorder in the bombed cities. Often the names and data of little children were lost and, by the time the mother or the parents could find them, the children



themselves had changed by growing up. Then government officials sent the family to an anthropological or genetic institute which could often give them the assurance that the displaced child really belonged to this family (Schwidetzky '49, Steffens '50).

However, such cases are but a very small part of the work of such institutes. Much more frequent are the cases of illegitimate children whose progenitors refuse to pay for them and similar forensic cases where the courts request expert opinion from anthropologists. The German Anthropological Society (*Deutsche Gesellschaft für Anthropologie*) has published a list of experts fully qualified both by training and experience; the latest edition (1952) contains the names of 35 anthropologists and human geneticists, some of whom are physicians, the others biologists. Some of these experts have established private laboratories of forensic anthropology, while others are connected with university institutes where younger anthropologists, whose salaries are paid for out of the fees charged, take part in the investigations. On the average, each expert on the approved list may take on about 75 cases per year. Thus about 2500 expert opinions are presented to the courts by anthropologists every year. More opinions are given by physicians who are not on the list of the German Anthropological Society because they have neither the education nor the experience necessary for fully qualified investigations. These are not blood-group determinations. Cases are sent to the anthropologists only when the blood groups, determined by institutes of serology, legal medicine, etc., have led to no definite conclusion, that is to say, the presumptive father could not be excluded.

The first anthropological opinion of this kind was given in the year 1926 by Professor Otto Reche who was at that time the director of the Anthropological Institute at Vienna. In the next decade the anthropological institutes, particularly at Berlin (Eugen Fischer, von Verschuer, et al.) and at Vienna (Weninger, Geyer, et al.), continued to develop the method. Other institutes participated in this work, collected and exchanged experiences, and trained younger human biologists. The courts came increasingly to trust in the new method which had helped to clear up so many cases. In 1931, the Supreme Court of Vienna decided for the first time that the non-admittance of an anthropological expert opinion was a defect in legal proceedings, and soon this was the general point of view in Germany as well (Harrasser '35, '50).

According to a recent inquiry in various countries, Germany and Austria are ahead not only in the development but also in the applica-

tion of the methods of forensic anthropology (Schwidetzky '51a). Only in Sweden and Denmark are they also well introduced into the administration of justice, but there are not so many referrals as in Germany. The Institute of Human Genetics and Race Biology at Uppsala, whose director is Professor G. Dahlberg, seems to have the only department of forensic anthropology in Sweden, and it renders about 25 to 30 expert opinions each year. In Czechoslovakia, German experts introduced the method during the occupation of that country, and a Czech anthropologist has continued to use it after the war (Valšík '49). In Poland and Switzerland as well the first opinions have been prepared by anthropologists (Pfannenstiel '53). In the United States, and in many other countries too, the method is almost entirely unknown. Sometimes physical anthropologists are requested to render an opinion in cases of supposed Negro descent, as, for example, when a child is to be adopted. But this is really more a matter of racial diagnosis than one of family descent, since only the child and not the parents is examined. In answer to the inquiry mentioned above (Schwidetzky '51a), an American geneticist wrote as follows: "I am amazed at the degree to which both anthropologists and the legal profession in Western Germany have developed the scientific aspect of the determination of paternity. I believe that is far ahead of anything done in this country."

After the war there was an immense increase in the number of referrals in Western Germany: many illegitimate children were born, many former soldiers when they returned home were confronted with offspring in their families whose progenitors they could not be or they believed themselves not to be. In recent years the number of cases has become more normal and in a better proportion to the number of available experts. And as scientific research revived in Germany, the further development of forensic anthropology took place. In its Mainz meeting in 1950, the German Anthropological Society devoted an entire day to lectures and discussions on this topic. In 1953, a special meeting for experts was held in Münster, arranged by the Institute of Human Genetics, which is now the most active center of research in human genetics in Germany. Its director, Professor von Verschuer, is the president of the German Anthropological Society at the present time. These special meetings of forensic anthropologists will be held every two years to exchange experiences and to discuss the results of continuing scientific research.

The method of determining paternity involves many hereditary traits



with the exception of blood groups which are determined in advance. Some of these traits with simple inheritance, such as eye color, hair form, or the ability to taste P.T.C., provide evidence to exclude the wrong father under some circumstances, but not with the same degree of certainty as is the case with blood groups. However, the principal part of the method consists in the comparison of the child, mother, and suspected progenitor(s) in a large number of complex polymeric traits whose hereditary nature has been established by twin and family research work but whose mode of inheritance is not known in detail (Kramp '39, '40, '42, '48, Loeffler '40). The greater the number of similarities between the child and the progenitor in question, the more probable it is that he is really the child's father. Thus it may be possible to determine the father positively (Vaterschaftsnachweis), while on the other hand by stating that blood groups and other monomeric characters we can exclude a suspected progenitor from being the father (Vaterschaftsausschluss).

In order to determine the total resemblance in hereditary traits it is recommended to consider as many of them as possible. In the "Instructions of the German Anthropological Society for Anthropological-Genetic Expert Opinions in Forensic Cases" (1949) 4 pages are devoted to the enumeration of hereditary traits which must be examined. These include the following groups: structure of the iris (including eye color), hair texture and hair growth patterns, form of the head (including the forehead), total face, eyes (including eyebrows, eye lashes, eye folds), nose (including nostrils and nasal wings), mouth and chin, ear, oral cavity (including teeth and tongue), hands and feet, papillary ridges on fingers, palms, toes, and soles), and physiological traits such as the ability to taste P.T.C. Photographs, at least of the head as seen from the front and from the side, must be taken and added to the expert opinion. Special photographs of the iris, ear, eye region, nose from below, hands, and feet are recommended, especially when there are important similarities between the child and the presumptive father.

It is obvious that not all of these traits have the same value in every case:

1. Traits which change greatly during growth, such as the form of the forehead, nose breadth or chin, are less important, but they must always be examined because there may be striking similarities.

2. Sex variability has also to be considered since the child is always

compared with individuals of both sexes, i. e. mother and presumptive father.

3. Those traits which are similar in the child and mother are less important for the comparison between the child and presumptive father. But they are not entirely a matter of indifference: if the child resembles the mother and the presumptive father, this is a more positive piece of evidence than when the child is similar to the mother and dissimilar to the presumptive father.

4. Similarity in traits of frequent occurrence do not lend the same evidence as do rarer traits.

5. Of course, such highly modifiable traits as body weight or chest circumference are of lesser importance.

Experience is needed to consider all these points of view, to know the variability by age and sex, the approximate frequency of the traits, the possible effects of environment and so forth. Therefore, the German Anthropological Society admits to its list only human biologists who have had three years of experience in an appropriate institute, and three expert opinions of each applicant are examined by a commission of 5 experts. An attempt is also made to clarify those cases in which two expert opinions are given whose results do not correspond. It may be mentioned that there have been but few cases of this kind where both experts have been admitted to the approved list of the Society.

It is obvious that the methods of determining paternity have not yet been exhausted. There are several avenues for future development: 1. New hereditary traits are being sought for. 2. An attempt is being made to determine more precisely the variability and frequency of the hereditary traits already known, thereby providing further evidence of special similarities. 3. Methods for the more precise summarization of the detailed findings are now under examination.

1. New hereditary characters are being sought for: though twin research has examined an immense number of morphological traits, some of them may have been overlooked or can be rediscovered for the purposes of forensic anthropology. Klenke ('51) examined the details of the palate from this point of view: the palatal ridges, the form of the *rapha mediana* and the *papilla incisiva*, the height and form of the palate can be used. Schäfer ('52) studied the uvula, Biegert ('53), the tongue Schwidetzky has settled the hereditary character of certain morphological variations of the skull such as the *crista supramastoidea*, *torus* or *sulcus*



*bregmaticus*, *depressio lambdoidea* and the *tubera parietalia*. Most impressive are the studies of Loeffler ('53) on the hair-streams of the forehead and neck. Rieger and Thums ('51) proposed an ophthalmological examination which has already given evidence in some paternity cases. This leads to pathological traits which sometimes clear up or decide a case.

Last but not least, the vertebral column may be mentioned here. It has been vehemently discussed in recent years. Kühne has assumed that the variations of the spine are determined by one pair of genes. There is a cranial and a caudal tendency in variations, and the caudal one is said to be dominant. Special expert opinions based on the spinal column (Wirbelsäulengutachten) were made by Kühne and other experts in paternity cases, especially during the years 1948-1950 (Bickenbach '47, Kühne '50). Variations in the spinal column were employed as excluding traits like blood groups, but some experts have also pointed to the positive similarities between parents and children (Ilchmann-Christ and Diethelm '53, Pratje '51). Lenz ('51a, '51b) rigorously criticized this method at the 1950 meeting of the German Anthropological Society, and it has since almost completely disappeared from the practice of forensic anthropology. The results of further research should be awaited. In the meantime, one paper has been published, and perhaps this is the beginning of a revindication of the trait (Ilchmann-Christ and Diethelm '53). In 113 paternity cases investigated by Lehmann, variations in the spinal column were examined independently by Ilchmann-Christ and Diethelm. Only in one case was there a certain contradiction between the two results, and the authors have also pointed to the positive similarities between the children and their parents. To be sure, such investigations are expensive, since 4 or more X-rays of the spine are needed. But in important cases which cannot otherwise be sufficiently cleared up they may give supplementary evidence to the courts.

In regard to Mendelian inheritance, the experience of forensic anthropologists has disqualified another trait as well: the Bonnevie formulae for digital ridges. The average number of ridges, the maximum and minimum and the differences between single fingers show similarities between relatives, but the trait cannot exclude a presumptive father, as the formulae pretend to do (Baitsch '53). There are too many discrepancies even between children and mothers which cannot be solved. At their Münster meeting, therefore, the anthropologists decided to no longer use the formula in their expert opinions.

2. An attempt has been made to determine more precisely the variability and frequency of the hereditary traits already known. This is a most important part of the research and probably most work is being done in this field.

The papers of Ehrhardt ('51) on the eye folds and those of Pfannenstiel ('52) on the traits of the mouth and chin will be mentioned first of all. They give the frequency of the traits by age groups. It is supposed, and this really seems to be quite certain, that they point to a frequent trend in individual development, but not all possibilities of individual changes by growth and age can be determined in this way. Examinations of the same individuals at different ages have to be carried out. This research has been started at the Institute of Human Genetics at Münster. Professor von Verschuer studied the same pairs of twins in 1924-25 and in 1950. The children of the first studies have now become adult, and the adults are now in old age. In this small but extremely valuable study the age changes in physiognomical features can be compared with the non-hereditary differences between monozygotic twins. The first paper (Gerhardt '52) already has verified very clearly the general experience of anthropological experts that the classification of morphological traits in terms of a pre-determined scheme is not sufficient. In the Instructions of the German Anthropological Society we find the following statement:

"By wedding oneself to a pre-determined scheme, one's glance is diverted from that which is essential, that is to say, the critical examination by *comparison*. In this latter case it is basically a question of the finer details of certain structures, of the *degree* of similarity and dissimilarity, which are to be observed in the distinguishing traits. Such observations cannot be forced into the framework of an already existing measurement blank but must be carefully noted in each individual case by a detailed description of form."

Beyond the precise verification of this experience, the twin studies show which different forms can be considered as similar from the genetic point of view. The same question is to be put to traits without considerable age changes. Much work in Germany is being done on the papillary ridges which are of such great importance in modern human biology. According to Kramp ('52) and to our general experience as well, similarity in special details are more important in paternity cases



than conformity to pattern-type. Different patterns can have similar detailed traits, and the same type of pattern in the child and presumptive father provides less evidence when the special structures are highly different. In the same way, the intrafamilial variability of palm ridges was studied by Ehrhardt ('53), that of the *planta* by Gieseler ('53). But also quantitative traits, such as the number of whorls or the height-breadth index of finger-patterns studied by Becker ('53) should not be completely neglected. In such traits similarity or dissimilarity can be determined only by statistical methods, and it is, therefore, particularly important to know their variability and frequency.

The same is true for anthropometry. Most experts take only certain measures and then only because of anthropological tradition. Keiter ('51a) has pleaded, however, for a rehabilitation of anthropometry and has developed an "anthropometrical diagnosis of descent" (anthropometrische Abstammungsdiagnostik) with approximately 50 anthropometrical traits. This diagnostic method of Keiter has been often criticized and rejected. In fact, however, an exact analysis of anthropometric data can give some evidence, as Schwidetzky verified for head measurements at the Münster meeting, and it is able to complete morphological comparison. Children and adults can well be compared when the deviations from the average of age and sex groups are taken into account: especially great deviations, similar in both the child and the presumptive father, can assist in determining the biological relationship.

3. Methods are being examined for the more precise summary of the detailed findings. The main trend in the development of forensic anthropology is the growing complication of the examinations. More and more traits are introduced, and, in general, the more recently introduced traits are the more difficult in method: it is easy to take finger-prints but more difficult to take toe-prints, as recommended by the Society's Instructions and now adopted by nearly all experts; the examination of the palate needs a plaster-cast; that of the iris, a special magnifier; Loeffler's hair-streams, a movable lamp (and, unfortunately, a good deal of time); the spinal column has to be X-rayed. Technical assistants may help during the morphological examinations, for instance in taking finger prints and photographs. The main part of the examination, however, must be done by the expert himself. The direct morphological comparison of child, mother and presumptive father, and the summary of the ever-increasing number of details in the final result

cannot be left to assistants. Therefore, the method cannot be too much mechanized and reduced to merely a technical procedure, and more and more experience and time are needed to prepare a fully qualified expert opinion.

As more and more details have to be summarized, it becomes increasingly important how the final result is obtained. In this respect, the existing Instructions of the Society (1949) are rather indefinite. According to these Instructions, all details have to be summarized in one of the degrees on a scale of probabilities as follows:

1. The probability that the presumptive progenitor is the real father borders on certainty;
2. It is highly probable that the presumptive progenitor is the real father;
3. It is probable that the presumptive progenitor is the real father;
4. It is impossible to reach any conclusions;
5. It is improbable that the presumptive progenitor is the real father;
6. It is highly improbable that the presumptive progenitor is the real father;
7. It is obviously impossible that the presumptive progenitor is the real father.

Lenz prefers other terms, and other experts are following his lead:

1. It is evident that the presumptive progenitor is the real father;
2. It is reasonable to suppose that the presumptive progenitor is the real father;
3. It is not evidently impossible that the presumptive progenitor is the real father;
4. It is reasonable to suppose that the presumptive progenitor is not the real father;
5. The presumptive progenitor is evidently not the real father;
6. It is evidently impossible that the presumptive progenitor is the real father.

These terms are perhaps more convenient for the judges, who are not accustomed to the theory and terms of probability.

In a modification of Loeffler's scheme (Loeffler '40), which employs

additional categories, these degrees of probability might be equated to the following statistical probabilities:

- 1 = > 99
- 2 = 91-99
- 3 = 66-90
- 4 = 35-65
- 5 = 10-34
- 6 = 9-1
- 7 = < 1.

But that is only one approach, and there is no exact basis for these equations. It is only a matter of practical experience just how the final result is to be classified. Even a verbal definition of the various degrees is lacking in the Society's Instructions. Schwidetzky ('51b) has attempted to do this by equating the degrees of the final result with the degrees of total resemblance, which is, in fact, the main basis of the summary:

Similarity — 3 = *Evidently impossible* in forensic cases. Though there are many deviations from the mother, the dissimilarities with the presumptive father exceed greatly the similarities. There are also striking discrepancies in traits whose mode of inheritance is well known or only approximately known.

Similarity — 2 = *Very improbable* in forensic cases. There are many and considerable differences between the child and the mother, but also more dissimilarities than similarities with the presumptive father. The similarities between the child and the presumptive father do not involve rare and striking traits.

Similarity — 1 = *Improbable* in forensic cases. There are more dissimilarities than similarities between the child and the presumptive father in traits differing from the mother, but the deviations from the mother are small and involve no traits whose mode of inheritance is known.

Similarity 0 = *No evidence* in forensic cases. The traits of the child which differ from those of the mother are partly to be found in the presumptive father. All



similarities involve frequent traits, but also the dissimilarities are not striking, since the deviations from the mother are small.

Similarity + 1 = *Probable* in forensic cases. There are more similarities than dissimilarities between the child and the presumptive father in the traits differing from the mother, but most similarities involve frequent traits.

Similarity + 2 = *Very probable* in forensic cases. Some of the similarities between the child and the presumptive father differing from the mother are striking, that is to say, they involve rare details or the similar structure of whole morphological regions.

Similarity + 3 = *Evident* in forensic cases. There are still more striking similarities between the child and the presumptive father; the child resembles more the presumptive father than the mother.

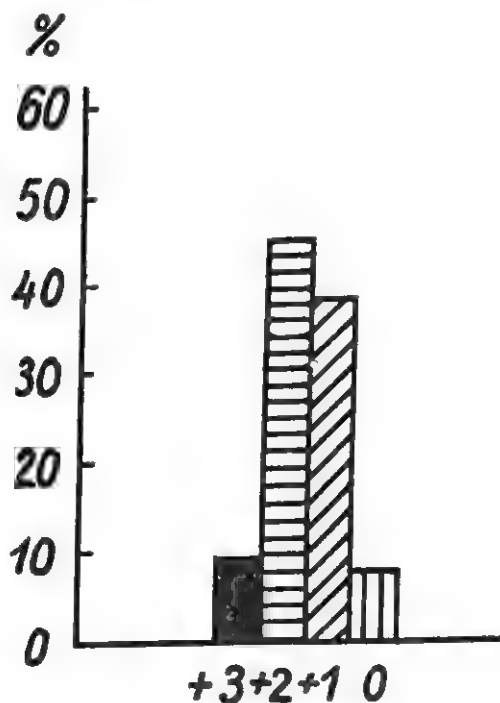


FIG. 1. Distribution of the degrees of total similarity between children and father in unquestionable families (100) children).

Note that the degree "0" is also represented in unquestionable families.

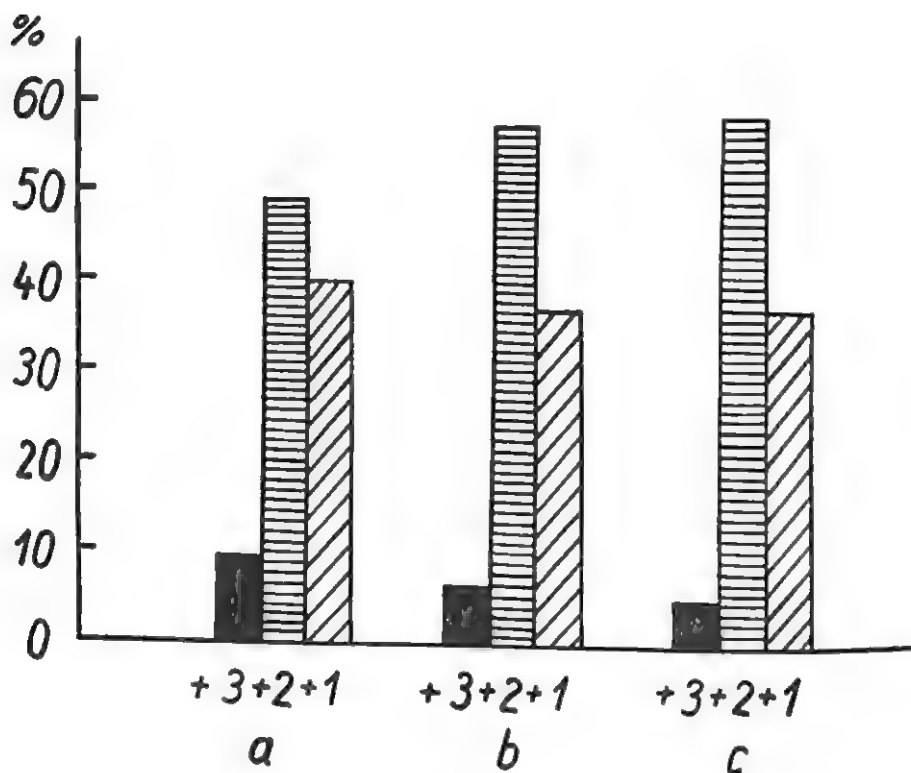


FIG. 2. Distribution of the positive degrees of total similarity between children and "right" fathers.

(a) In families.

(b) In forensic cases with one presumptive progenitor.

(c) In forensic cases with two presumptive progenitors.

Note the similarity of distribution in families and forensic cases.

But these are vague definitions too. It is one of the most vehemently discussed problems of forensic anthropology whether it is possible to give a statistical formulation to the final result. The first method of this kind was developed by Essen-Möller ('38, Essen-Möller and Quensel '39) and applied by Geyer ('38). Essen-Möller calculates for each trait a "Critical Value" (Kritischer Wert) which may be defined as  $\frac{Y}{X}$ , where  $X$  is the frequency of conformity between the children and the "right" father and  $Y$  the frequency of the trait in the average population or in the "wrong" fathers. The probability of finding the "right" father by this trait is then



$$P_r = \frac{1}{1 + \frac{Y}{X}} \quad (1)$$

The probability of finding the "right" father by several traits (1, 2, 3, etc.) is

$$P_r = \frac{1}{1 + \frac{Y_1}{X_1} \cdot \frac{Y_2}{X_2} \cdot \frac{Y_3}{X_3} \cdot \dots} \quad (2)$$

When there are two presumptive father (*I, II*), of whom one is the real progenitor, there is a greater probability of finding him, that is to say, the probability is higher than for a single man.

$$P_{r_i} = \frac{(\frac{Y}{X})_{II}}{(\frac{Y}{X})_I + (\frac{Y}{X})_{II}} \quad (3)$$

To this several serious objections have been made (Ludwig '51, Weninger '49). The two most important ones may be mentioned.

1. The "critical values" are multiplied in formula (2). This would be valid only if there were no correlation between the traits. But even if the correlations between all the traits considered in paternity cases were known (up to now they are not), it is practically impossible to account for them in the formula. Thus, the calculation has to restrict itself to non-correlated traits, foregoing many other traits, possibly important ones.

2. The "probabilities" of the Essen-Möller formula are not real statistical probabilities, since they do not consider the statistical error.

Keiter ('53b) has replied to these arguments that Scheidt had calculated hundreds of correlations between morphological traits of the face and had found but few correlations of a low degree. Wichmann ('51) used a much greater number of traits than formerly customary and could quite well separate the "right" from the "wrong" fathers, as determined in 120 paternity cases by morphological comparison.

Further methods have been proposed or examined. Keiter ('51a, b, '53a) has developed two statistical methods.

1. The diagnosis of descent by correlations (Korrelationsstatistische Abstammungsdiagnostik). It is applicable only to quantitative characters, but also many morphological traits can be quantified (high-low,

big-small, etc.). Keiter always takes 7 degrees. The correlation between the child and the presumptive father is calculated for each case, and the variability of correlation-indices is determined. There is some over-

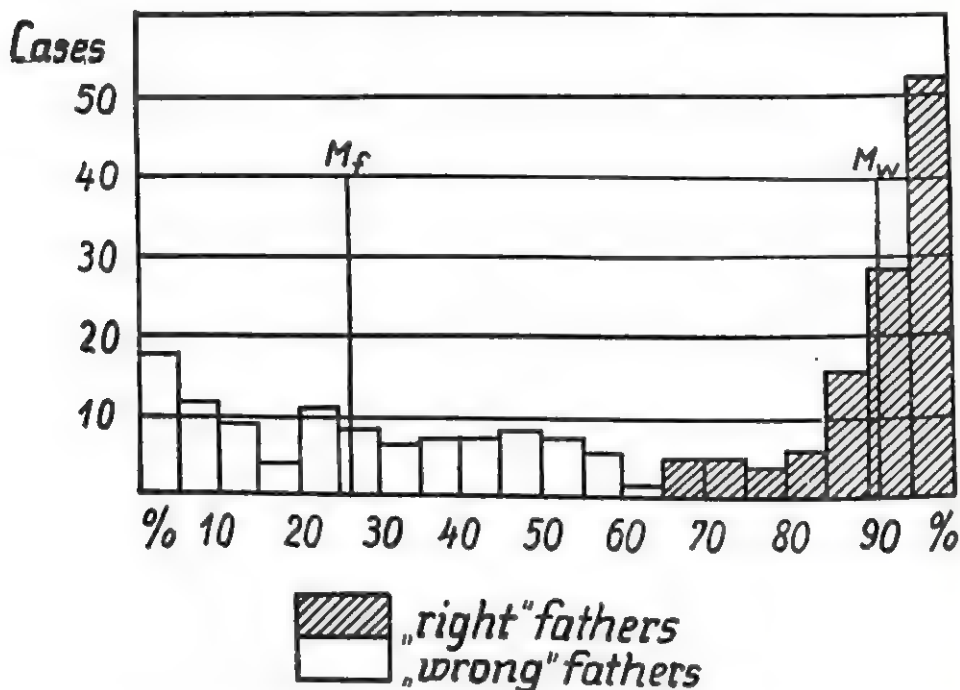


FIG. 3a. The distribution of the degrees of probabilities according to the 2nd Essen-Möller formula. (216 presumptive fathers in 120 forensic cases, 31 traits). "Right" and "wrong" fathers are determined by total morphological comparison. Note that there is no overlapping of the distributions in these 120 cases. However, as the distributions are contiguous, an overlapping may occur in other cases. There are also probabilities  $> 50$  for "wrong" fathers, but no probabilities  $< 50$  for "right" fathers.

$M_w$  = Average of the "right" fathers.

$M_f$  = Average of the "wrong" fathers.

(after Wichmann)

lapping between "right" and "wrong" fathers determined independently by morphological comparison, but the difference between the two groups is quite clear.

2. The "Logarithm of Paternity" (Vaterschaftslogarithmus) determines for each trait the similarity between the child and the presumptive father on a 7-point scale, at the same time taking the similarities between the child and the mother into account. The different combinations are



classified according to their value as evidence (Keiter '51b). Ludwig ('51) has proposed the use of discriminant functions to separate "right" from "wrong" fathers. This method can also be applied only to quan-

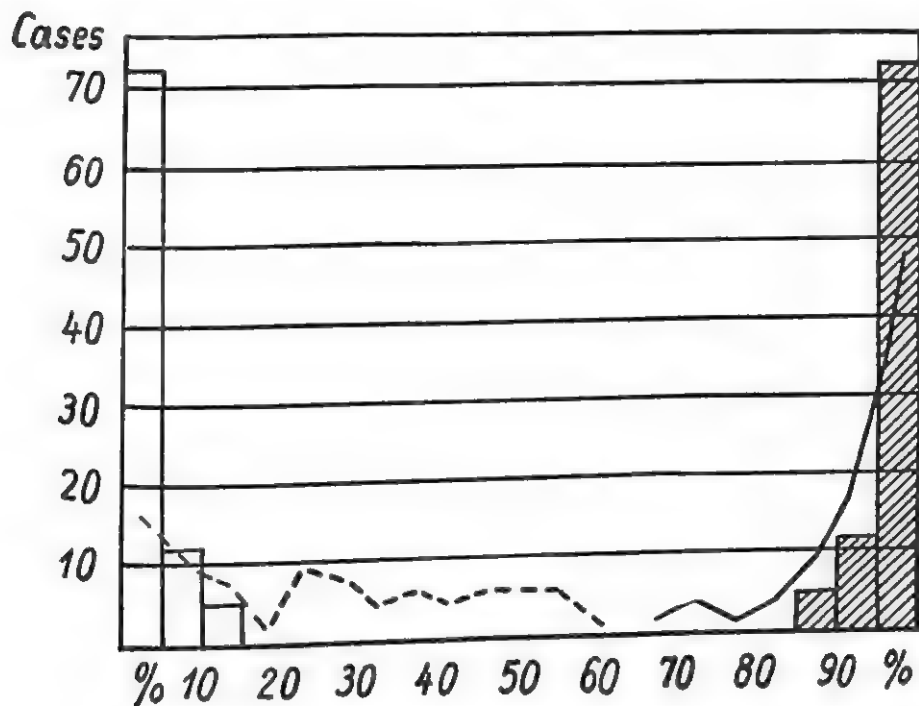


FIG. 3b. The distribution of the degrees of probability according to the 3rd Essen-Möller formula. (Two presumptive fathers of whom one is the real progenitor).

Note that the distributions are now well separated.

There is no overlapping and contiguity.

— Distribution of the "right" fathers.

- - - - - Distribution of the "wrong" fathers according to Fig. 3a.

(after Wichmann)

titative traits of normal distribution. Apparently no one has yet attempted to use it. Schwidetzky ('53) has used a coefficient of likeness, and it is one of the main purposes of her family investigations (Schwidetzky '51b) to define more exactly the "total resemblance" and its variability in families in which it may reasonably be assumed that the fathers are in fact the real progenitors. Only family research can really prove or disprove the validity of statistical methods of sum-

marizing. When they are applied to "right" and "wrong" fathers in paternity cases, there may be a selection of "good" cases, that is to say, those which could be well decided. But there is always a number of undecided cases (approximately 10%) whose presumptive progenitors cannot be classified either as "right" or as "wrong" fathers. Total resemblance "O" between the child and the father also occurs in unquestioned families. Thus only family research can indicate the whole variability of total resemblance between relatives and thus define more exactly the degrees of probability in determining the "right" progenitor.

Most experts refuse to use statistical methods in the opinion itself. There was a long discussion on this subject at the Münster meeting. It was pointed out that only a portion of the traits considered in forensic anthropology can be proved statistically and that it is more important to *see* similarities and differences than to *calculate* them. A rigid classification of traits which is inevitably involved in statistical analysis may indeed conceal the real similarities, and there are often morphological details and special structures which have never been described and which are too rare to be studied statistically. But it is just such traits and structures which are of the greatest importance in paternity cases.

This is certainly true. Perhaps, on the other hand, some experts are too hostile to the use of statistical methods in regard to the practice of forensic anthropology. Some arguments in their favor may be mentioned here.

1. General conclusions and a theory of the method of similarity are impossible without statistical analysis, and, of course, general results are also of use in the practice of forensic anthropology. For example, statistics has verified the practical experience that expert opinions are somewhat more positive for boys than for girls and that there is no important difference in certainty for children of three years and for those older than three; increased difficulties exist only for younger children, partly on account of their undeveloped traits, partly on account of technical difficulties in taking finger-prints, plaster-casts, standardized photographs, taste tests, etc. There is also a similarity among the various lovers of the same woman, and it has been proved that the analysis of similarity is more successful in determining positively the "right" fathers than in excluding the "wrong" (Keiter '53a, Schwidetzky '51b).



2. Statistics help in establishing more exactly similarities and dissimilarities, especially in quantitative traits. It is true that statistics require a precise classification of traits which do not suit completely the practical purpose of the method. But a large number of traits are well adapted to statistical analysis, such as measures and indices, or the present-absent traits which are not too rare in the average population. Many details can be settled more precisely, and even further details may be discovered by statistics. Certainly no expert would reject statistics for the critical investigation of single traits, although heretofore it has been possible only for a few of them.

3. There is a general trend in the natural sciences (and last but not least in genetics) to quantify their methods, and if statistics are admitted to the exact analysis of single traits, it is impossible to prevent their application to the summary of details.

It is true that none of the present statistical methods are fully satisfactory. Only a portion of the comparison of children and parents is involved. Such methods do not consider the similarities between the child and the mother, or they are unable to treat quantitative traits simultaneously with pure descriptions of form. They cannot see the wholeness of individual structures, being only able to sum up certain details in a mechanical fashion. I believe that it will be forever impossible to cover by statistical summaries all the details which are now used in forensic anthropology. There will be a better approach only with the further development of methods. But that portion of the results which can be expressed in an exact manner (in the sense of mathematics) should not be expressed inexactly. Perhaps at some time in the future there will be sufficiently exact proofs to decide most cases. Of course, the eye, the "morphological glance" can never be dispensed with, because the traits have first to be determined and classified before statistical analysis can proceed.

Today, about 10 per cent of the paternity cases remain undecided. The aim of the method of determining paternity must be that all cases can be cleared up and that the share of the high probabilities will become greater and greater. Indeed, the highest degree of probability is not necessary for the judge in all cases; often the mere presence of some positive or negative evidence suffices. However, for the experts it is much more satisfying to have full certainty. But already today one can say that "*pater semper incertus*" is no longer true.

## BIBLIOGRAPHY

- BAITSCH, H. 1953 Zum Problem der Erbformelberechnung im Tastleistensystem. *Zeitschrift für menschliche Vererbungs- und Konstitutionslehre*, 31: 352-358.
- BAUERMEISTER, W., AND M. KÜPER 1942 Die erbbiologische Abstammungsprüfung. *Fortschritte der Erbpathologie*, 6: 144-212.
- BECKER, E. 1953 Der Formindex der Papillarmuster im anthropologisch-erb-  
biologischen Vaterschaftsnachweis. *Homo*, 4: 18-27.
- BICKENBACH, W. 1947 Der genetische Wirbelsäulenvergleich. *Klinische Wo-  
chenschrift*, 24-25: 406-408.
- BIEGERT, J. 1953 [Paper read at the Münster meeting of forensic anthropol-  
ogists. Not as yet published].
- EHRHARDT, S. 1951 Über die Deckfalte am menschlichen Auge. *Zeitschrift für  
Morphologie und Anthropologie*, 43: 163-172.
- 1953 [Paper read at the Münster meeting of forensic anthropologists.  
Not as yet published].
- ESSEN-MÖLLER, E. 1938 Die Beweiskraft der Ähnlichkeit im Vaterschaftsnach-  
weis. Theoretische Grundlagen. *Mitteilungen der Anthropologischen  
Gesellschaft Wien*, 68: 9-53.
- ESSEN-MÖLLER, E., AND C.-E. QUENSEL 1939 Zur Theorie des Vaterschafts-  
nachweises auf Grund von Ähnlichkeitsbefunden. *Deutsche Zeitschrift für  
Gerichtliche Medizin*, 31: 70-96.
- GERHARDT, K. 1952 Altersveränderungen der Physiognomie bei Zwillingen.  
*Homo*, 3: 21-31.
- GEYER, E. 1938 Die Beweiskraft der Ähnlichkeit im Vaterschaftsnachweis.  
Praktische Anwendung. *Mitteilungen der Anthropologischen Gesellschaft  
Wien*, 68: 54-87.
- GEYER, E., AND K. TUPPA 1941 Vom Wert der Merkmale im anthropologischen  
Vaterschaftsbeweis. *Anthropologischer Anzeiger*, 17: 273-285.
- GIESELER, W. 1953 [Paper read at the Münster meeting of forensic anthro-  
pologists. Not as yet published].
- HARRASSER, A. 1935 Ergebnisse der anthropologisch-erbbiologischen Vater-  
schaftsprüfung in der österreichischen Justiz. *Mitteilungen der Anthro-  
pologischen Gesellschaft Wien*, 65: 204-232.
- 1950 Der anthropologisch-erbbiologische Vaterschaftsnachweis als ge-  
richtliches Beweismittel. *Neue Juristische Wochenschrift*, 3: 561-565.
- ILLCHMANN-CHRIST, A., AND L. DIETHELM 1953 Eine Studie über den' so ge-  
nannten genetischen Wirbelsäulenvergleich. *Zeitschrift für menschliche  
Vererbungs- und Konstitutionslehre*, 31: 431-462.
- KAHLICH-KOENNER, D. M. 1951 Praktische Erfahrungen bei der Anwendung  
der Essen-Möller'schen Formel in Wiener Vaterschaftsuntersuchungen.  
*Homo*, 2: 58-61.
- KEITER, F. 1951a Entwicklungsmöglichkeiten des anthropologisch-erbbiolo-  
gischen Abstammungsnachweises. *Homo*, 2: 65-68.
- 1951b Empirische Untersuchungen über den Vaterschaftsbeweiswert

- aller theoretisch möglichen Merkmal-kombinationen bei Mann, Mutter und Kind.* Homo, 2: 158-164.
- 1953a Über die Gesamtähnlichkeit von Eltern und Kindern. Homo, 4: 63-68.
- 1953b [Paper read at the Münster meeting of forensic anthropologists. Not as yet published].
- KLENKE, W. 1951 Die Gaumenfalten im Vaterschaftsnachweis. Homo, 2: 69-72.
- KRAMP, P. 1939 Der erbbiologische Abstammungsnachweis. Der Biologe, 8: 381-394.
- 1940 Der erbbiologische Abstammungsnachweis. Der Biologe, 9: 281-298, 364-381.
- 1942 Der erbbiologische Abstammungsnachweis. Der Biologie, 11: 87-95.
- 1948 Anthropologische Vaterschaftsdiagnose. Grenzgebiete der Medizin, 1: 221-232.
- 1951 Bibliographie zur anthropologisch-erbbiologischen Abstammungsprüfung. Homo, 2: 76-83.
- 1952 Familienähnlichkeiten des Hautleistensystems und ihre forensische Bedeutung. Homo, 3: 175-177.
- KÜHNE, K. 1950 Genetischer Wirbelsäulenvergleich. In: Ponsold, A., Lehrbuch der gerichtlichen Medizin, 392-404, Stuttgart.
- LAUER, A. 1952 Die serologische Aufklärung des Falles Aller. Homo, 3: 152-153.
- LENZ, F. 1951a Kritik der reinen Wirbelsäulenmethode. Zeitschrift für Morphologie und Anthropologie, 43: 9-20.
- 1951b Kritische Gedanken zur Wirbelsäulenmethode nach Kühne. Homo, 2: 53-55.
- LOEFFLER, L. 1940 Erbbiologische Ermittlung der Abstammung (Vaterschaftsdiagnose). In: Just, G. (Ed.), Handbuch der Erbbiologie des Menschen, 2: 321-359, Berlin.
- 1953 [Paper read at the Münster meeting of forensic anthropologists. Not as yet published].
- LOEFFLER, L., AND K. GERHARDT 1952 Der Fall Aller. Homo, 3: 148-151.
- LUDWIG, W. 1951 Zur Theorie der Essen-Möller'schen Methode. Homo, 2: 55-58.
- PFANNENSTIEL, D. 1952 Zur Morphologie und Genetik der Mund- und Kinnregion. Archiv der Julius Klaus-Stiftung, 27: 1-67.
- 1953 Anthropologische Gutachten im Vaterschaftsprozess. Schweizerische Juristen-Zeitung, 49: 101-106.
- PRATJE, A. 1951 Erfahrungen mit dem "Genetischen Wirbelsäulenvergleich." Homo, 2: 50-53.
- RIEGER, H., AND K. THUMS 1951 Augenärztliche Untersuchungen im Rahmen des anthropologisch-erbbiologischen Vaterschaftsnachweises. Wiener Medizinische Wochenschrift, 101: 594-601.
- SCHÄFER, U. 1952 Die Uvula palatina. Ein Merkmal zur Verwendung in erbbiologischen Abstammungsprüfungen. Zeitschrift für Morphologie und Anthropologie, 44: 201-210.
- SCHWIDETZKY, I. 1940 Ein neues Anwendungsgebiet des Abstammungsnachweises. Homo, 1: 170.



- 1951a Ergebnis einer Umfrage über den Stand der Abstammungsprüfung im Ausland. *Homo*, 2: 49-50.
- 1951b Untersuchungen an Familien mit unfraglichen Vätern zur Sicherung der Methode der Vaterschaftsdiagnose. *Homo*, 2: 72-76.
- 1953 [Paper read at the Münster meeting of forensic anthropologists. Not as yet published].
- STEFFENS, CH. 1950 Identifizierung von Kriegsfindelkindern mit Hilfe von erbbiologischen Ähnlichkeitsgutachten. In: *Moderne Biologie*, Festschrift für H. Nachtseim, 230-235. Berlin.
- TUPPA, K. 1951 Über die Bedeutung der relativen Häufigkeit wahrer Väter für die Essen-Möller'sche Formel. *Homo*, 2: 114-117.
- VALŠÍK, J. A. 1949 Quelle est la valeur de la méthode d'Essen-Möller et Geyer, pour l'examen critique de la paternité constatée? *Zprávy anthropologické Společnosti*, 2: 41-45.
- VON VERSCHUER, O. 1953 Die erbbiologisch-anthropologische Vaterschaftsbeurteilung, ihre wissenschaftliche Begründung und verantwortliche Anwendung. *Zentralblatt für Jugendrecht und Jugendwohlfahrt*, 60: 45-52.
- WENDT, G. G. 1951 Quantitative Fingerleistenmuster im Vaterschaftsgutachten. *Zeitschrift für menschliche Vererbungs- und Konstitutionslehre*, 30: 403-408.
- WENINGER, M. 1940 Zur zahlenmässigen Erfassung der Ähnlichkeit im naturwissenschaftlichen Vaterschaftsnachweis. Eine kritische Auseinandersetzung mit der Formel von E. Essen-Möller und ihrer praktischen Anwendung. *Mitteilungen der Anthropologischen Gesellschaft Wien*, 78-79: 33-58.
- WICHMANN, D. 1951 Erfahrungen mit der Essen-Möller'schen Methode. *Homo*, 2: 61-64.





## THE DEPOPULATION OF YAP

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IN much of the world, the spread of modern civilization has brought about the assimilation, depopulation or extermination of many small non-literate societies. Foreign diseases have become rampant among these peoples, along with wars, apathy and disorganization.

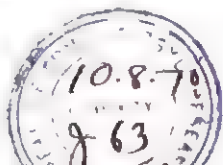
One such depopulation has gone on for perhaps a century on Yap, in western Micronesia. Yap is a cluster of hilly islands with a total area of 38.67 square miles, all enclosed within a single coral reef. Its inhabitants are typical of the high islanders of the central Pacific in that they eat mainly root crops from their gardens and fish and shellfish from the sea. Their social organization strongly emphasizes rank, with elaborate protocol and restrictions on the intermarriage and interdining of persons of high and low degree (Schneider, '53). Among the objects most treasured by the Yapese is their famous "stone money." This rich and intricate culture is still remarkably well preserved by a society of only a fraction of its former numbers.

The living islanders say that the depopulation followed a period of overpopulation which we consider to have occurred before 1850. Yap was then so crowded that disinherited and destitute men and even their families lived miserably on rafts in the mangrove swamps. It is said that sometimes 4 hungry men had to make a meal from a single coconut. A crude maximum estimate of the population of Yap at that time can be derived from a detailed map of 3 typical villages, made in the field by one of us (Schneider). Numerous platforms of coral rock are indicated on this map, and today represent both abandoned and occupied

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dwelling sites. Taking the most sparsely populated village as representative of the entire land surface of Yap, one may estimate the total number of house sites now present in the islands. If each site was occupied by an average of 4 people, and if all sites were ever inhabited at one time, we obtain a grand total of 51,000 islanders at the peak of overpopulation.

If 51,000 people ever actually lived on Yap, the population density would have been about 1,300 per square mile. Comparable densities on the most crowded Micronesian islands today are given in the 1952 report on the administration of the Trust Territory of the Pacific Islands, by the United States to the United Nations. Among these densities are Nama (2,093), Losap (1,892), Eauripik (1,477), Pingelap (914) and Kapingamarangi (892). These values are of the same order of magnitude as the estimate for Yap, but all of them apply to low-lying islands whose comparability with Yap is limited. The inland hilltops of Yap do not permit intensive cultivation, while most low islands are more uniformly arable. Relative to its land area, too, Yap has less extensive tidal flats for fishing than do most low islands. Finally, all of the house platforms in Yap may never have been simultaneously occupied. If an entire family dies out, its ghosts are believed to haunt their former homestead, so that other Yapese are afraid to move in. For all of these reasons, 51,000 may be an excessive estimate of the former population of Yap.

We cannot follow quantitatively the earlier years of the depopulation, but table 1 shows its continuation from 1899 to 1946. Although most of the population totals in this table are the direct results of various censuses, others had to be calculated indirectly. For several census years in the Japanese period, Yap was part of a district or administrative aggregate of western Micronesian islands, of which Yap's own population comprised 61% in 1930. For 1935, the Yap total was obtained by subtracting the number of Chamorros then living in Yap from the total number of non-Japanese there. This figure was again very nearly 61% of the district population. Because of this resemblance to the percentage for 1930, the Yap totals for 1920, 1925, 1936 and 1937 are taken as 61% of the district totals for these years.

The existence of this depopulation has been recognized by all three of the nations governing Yap during this century: Germany, Japan and the United States. German authors of official reports from Yap to the Reichstag, from which the 1900-11 census totals were taken, primarily



TABLE 1  
*Successive Population Totals of Yap Islanders*

CENSUS YEAR	GOVERNING POWER	RATE OF CHANGE		SOURCE OF DATA
		TOTAL POPULATION	PER YEAR IN PERCENT	
1899	Spain	7,808	—	Catholic mission data after Yanaihara ('39)
1900	Germany	7,464	—4.4	German government
1903	"	7,156	—1.4	" "
1905	"	6,641	—3.7	" "
1910	"	6,328	—1.0	" "
1911	"	6,187	—3.8	" "
1915	Japan	5,790	—1.6	Matsumura ('18)
1920	"	4,988	—3.0	61% of Yap district total in Yanaihara ('39)
1925	"	4,401	—2.5	"
1930	"	3,863	—2.6	Nanyo Gunto ('32), vol. 2
1934	"	3,665	—1.3	Japanese Government Annual Report ('36) to League of Nations Mandates Commission
1935	"	3,556	—3.0	Recomputed from Yanaihara ('39)
1936	"	3,467	—2.4	61% of Yap district total in Yanaihara ('39)
1937	"	3,391	—2.3	"
1946	U. S.	2,582	—3.0	Census by the authors
1947	"	2,607	+1.0	"
1948	"	2,625	+0.6	"
1949	"	2,694 (?)	+2.4 (?)	Marshall ('53)
1950	"	2,720	+1.1	"
1951	"	2,774	+1.9	"

considered the medical aspects of the decline, and attributed its long duration to epidemics and a consequent high mortality among the Yapese. The chief Japanese work on the depopulation was carried out by Fujii ('34) in response to queries from the League of Nations Mandates Commission to the Japanese government. His studies dealt with the health of the Yapese, both in its effects on mortality, and on their fertility.

Since the American occupation in 1945, two studies of the demography of Yap have been carried out. One was an unpublished census of Yap by John Useem in 1946. The second was the field research on which much of the present paper is based. It was part of the Coordinated Investigation of Micronesian Anthropology (CIMA), as described by Murdock ('48A, '48B). One of the many anthropological organizations which sent investigators into Micronesia was the Peabody Museum of Harvard University. The Harvard project was financed both by the museum and by the Office of Naval Research, and was carried out by the authors, together with Dr. William D. Stevens. A joint report to the Pacific Science Board, National Research Council, was a preliminary account of the findings presented here (Hunt et al., '49).

In 1949, the Navy hospital ship U. S. S. *Whidbey* visited Yap, and its staff carried out medical examinations, by both clinical and laboratory techniques of 2,193 islanders. McNair et al. ('49) have published the findings of this survey.

Thanks to Dr. H. L. Marshall, Director of Public Health, Trust Territory of the Pacific Islands, population totals for Yap in 1949, 1950 and 1951 are appended, even though he has doubts as to their accuracy.

#### DEMOGRAPHIC METHODS

All of the foregoing sources are incorporated into the present paper, especially material from the census by the Harvard expedition of 1947-48. The field methods used in this census were a function of the smallness and isolation of Yap and the peculiarities of its social organization. Two of the authors (Kidder and Hunt) traveled together from village to village with parties of Yapese census interviewers. Two or more small hamlets could usually be reached in a day, or else one larger community. Since modern Yap has about 100 inhabited villages, it was impossible to define one enumeration day for the whole area. Instead, the date of the interviewing for a particular village was taken as its enumeration day.

Errors of enumeration almost inevitably bedevil census workers. Where a population is enumerated on successive days, internal migration during the census may lead both to incomplete registration and to double enumeration. Fortunately, external migration was not a source of error because of the isolation of the islanders. Errors were controlled by a series of checking devices which made use of two features of Yapese social organization. One was its grading by sex and age, and the other was its patrilocal extended family. For each sex, the age-grading system

isolates groups of approximate age-mates at formal gatherings. At each village, a Yapese census interviewer would obtain a list of all the villagers in each age grade from the local inhabitants. Secondly, and never concurrently with the first list, an interviewer would obtain a list of all the occupants of each familial residential area. Before leaving the village, both lists were cross-checked with the incoming individual census schedules. All discrepancies were corrected before leaving the village.

Each individual census schedule was then used for secondary checks on the accuracy of enumeration. Every schedule contained the names of many persons other than the enumeratee himself. These others included the name and (if living) the present village of the enumeratee's real and foster parents, all progeny of his mother besides himself, his present and divorced spouses, and real and adopted children. If any of these individuals had died since the beginning of the American occupation in 1945, his death was checked against all of the other independent sources of vital statistics. Cross checking revealed whether schedules were available on every living relative of the enumeratee, and whether common data on the two schedules were in agreement. If the villages of these relatives had not yet been visited, each relative's name was entered on a "loose ends" file to be cleared up during later enumeration days.

In each of the 10 districts into which Yap had been divided during the German regime, the authors hired a vital statistics reporter. In obtaining primary household or extended family lists, the occurrence of any pregnancy or death since the American occupation was noted. Finally, all of these events were checked against the births and deaths which had been entered in the register of vital statistics kept by the American administrators.

The interviewers attempted to account for the time and outcome of every pregnancy of every living female Yapese. Not only the occurrence, but the dates of most of the live births during the Japanese period were obtained from the remarkably complete, original registers of vital statistics kept by the Japanese policemen in Yap. The terminal dates of other pregnancies were interpolated as accurately as possible for each woman, on the basis of well-known events in recent Yap history such as typhoons and major ceremonies, and also through comparisons of these dates with the years of birth of living persons which had been entered in the Japanese records.

Before the American occupation in 1945, Yap men were much more



likely to go overseas than the women. The number, time and duration of such absences were therefore recorded for every male. Under the Americans, migration has been virtually limited to the few young adults who have gone temporarily to Guam, Truk or Fiji for training as teachers, nurses, or native medical practitioners.

The Harvard census produced a body of demographic information on a non-literate society which is relatively abundant and accurate. The year of birth of nearly all of the islanders born since 1914 is known, and even the ages of other individuals born since the beginning of the Spanish occupation in 1885 are fairly accurate because of the close correspondence of the Yapese age-grading system with chronological age. In addition to the census, the physical anthropologist (Hunt, '50) measured series of both sexes, and considerable ethnographic information was gathered by Schneider, Stevens and Hunt.

#### HYPOTHESES CONCERNING THE DEPOPULATION

The size of a population of organisms can be compared to the level of a lake, with births and immigration as the inflow, and emigration and deaths as the drainage. In a declining population, the losses evidently exceed the gains. The remainder of this paper deals with a series of factors which in some cases probably influence demographic changes in human societies, together with our attempts to evaluate their importance in Yap. These factors include the following:

High and disadvantageous mortality because of diseases and neglect.  
Inadequate reproduction because of:

Male absenteeism from Yap

Malnutrition and physical deterioration

Intestinal parasites

Reproductive pathologies and abortions

Patterns of copulation, contraception, fecundity and fertility.

Finally, the increase in the birth rate in recent years is related to improvements in health, morale, and the Yapese way of life.

#### DISEASES, NEGLECT AND MORTALITY IN YAP

The major causes of death among the Yapese are fairly typical of those found among Pacific islanders, and include both chronic and epidemic infections. Some of the peaks in the annual rates of depopu-

lation, as recorded in table 1, seem to be related to these epidemics. These rates have been calculated from the compound interest formula. Letting  $n$  equal the number of years between censuses,  $P_t$  the terminal census total, and  $P_i$  the initial one, we solve for  $r$ , which is the geometric mean rate of change per annum:

$$P_t = P_i(1 + r)^n.$$

For the entire interval from 1899 to 1946, the mean rate of decline is  $-2.3\%$  per year. The rates between population totals in table 1 vary considerably from this value. Some, but not all, of this variation probably occurs because different methods of census enumeration were employed for different years. Without considerable errors, the data do not fit this or any other semilogarithmic curve. When measurements of somatic growth or numerical changes in living populations fit such curves, biologists are likely to assume that factors affecting these trends have operated uniformly through time. Such uniformity seems not to have been true of Yap, partly because of the episodic effects of epidemics on mortality.

For the German period (1900-1914), the intervals with the severest depopulation coincide with 2 known epidemics. In October, 1903, 50 Yapese died of some kind of influenza, and from 1909 to 1911, a typhoid epidemic raged. Yapese informants described 3 epidemics during the Japanese period (1914-1945), but the exact disease in each case is uncertain. The first epidemic may have been influenza in 1924, the second diphtheria in 1925, and the third amebic dysentery in 1936. The census data for Yap during these years are too incomplete and indirect to show the effects of these later epidemics.

For the period 1917-29, Fujii ('34)\* presents the average annual numbers of births and deaths. If we assume that the depopulation at this time represented only the excess of deaths over births, approximate average crude birth and death rates can be calculated for the year at the midpoint of this interval (1923) by the compound interest formula. The rate of decline from 1915 to 1930 by this formula is  $-2.66\%$  per year. Using this rate, the 1923 population is estimated to have been 4,667. This number serves as the basis for the average birth and death rates for 1917-29. From Fujii's data alone, such rates are calculated for 1930, and for 1946 to 1951 they are computed from American sources.

Table 2 indicates that the crude death rate was about 40 per thousand in the Japanese period. The range of national crude death rates for

TABLE 2

*Yap Births, Deaths and Calculated Crude Rates, 1917-1951*

YEARS	POPULATION TOTAL	ANNUAL LIVE BIRTHS	CRUDE BIRTH RATE	ANNUAL DEATHS	CRUDE DEATH RATE
1917-29 (estimated, 1923)	4,667	67	14.4	181	38.8
1930	3,863	59	15.3	167	43.3
1946	2,582	70	27.1	84	32.6
1947	2,607	82	31.4	59	22.6
1948	2,625	66	25.2	53	20.2
1949	2,694 (?)	71	26.4	48	17.8
1950	2,720	97	35.6	54	19.9
1951	2,774	100	36.1	48	17.3

1940, cited in Dublin et al. ('49), is from 9.2 in New Zealand to 26.5 in Egypt. It is therefore evident that the Yap islanders experienced a high mortality under the Japanese. With such a death rate, only immigration or a correspondingly extreme birth rate could have arrested the depopulation. Under the American regime, however, the death rate has fallen by about 50%.

Very little is known of age-specific death rates during the Japanese period or earlier. Price ('36) alleges that infant mortality during the Spanish regime, prior to 1900, was an improbable 800 per thousand, and that it was still at 390 per thousand in 1929. On presumably better authority, however, Fujii ('34) says that in 1417 births from 1917 to 1929, the infant mortality was 133 per thousand, mainly as a result of acute enteritis. In the United States nearly a century ago, comparable infant death rates prevailed (1 in 6, according to Dublin et al., '49). Since the American occupation of Yap, infant mortality has decreased, as shown later in abridged life tables for both sexes.

The greatest killer of the older islanders is probably pulmonary tuberculosis. It is cited by the Germans, and Fujii found it to have been active in 8 of the 9 Yapese whom he examined at necropsy. The *Whidbey* survey made mass chest roentgenograms and skin tuberculin tests in Yap, and McNair et al. ('49) state that 95% of a sample of 1,112 Yapese showed positive tests with both first and second strength purified protein derivative. The percentage increased sharply after the age of 10. Active pulmonary tuberculosis, however, occurred mainly in individuals more than 50 years of age, and was of the adult or reinfection type.



The evidence suggests that at least some of the Yapese have resistance to this disease, but without adequate histories of individual infections, this conjecture cannot be proven.

Other important chronic diseases of the Yapese are leprosy and intestinal parasites, and formerly included yaws. Over 50 Yapese have been sent to a leprosarium on Tinian where modern treatments are being given to them. The parasitic infestations and yaws of the Yapese will be considered later.

A total of 196 Yapese died during the period 1946-48, so that the transformation of their age-specific mortality into life tables is questionable because of possible sampling fluctuations of the data. The precision of the original vital statistics, however, made these computations seem worth while. For ages 0-5, the tables were calculated by a method suggested by Greville ('43) because accurate data were available on Yapese infant mortality. Later ages were computed by the procedure of Reed and Merrell ('39). These tables represent the pattern of mortality at the time of transition from a decreasing to an increasing population.

In these tables, the expectations of life at birth resemble those of Venezuela in 1941-42 (Dublin et al., '49, p. 344), but unlike nearly all civilized populations, in Yap the females have a shorter expectation of life than the males. Female infants below the age of one year are three times as likely to die as males, but at later ages, children of both sexes show similar mortality. In the earlier childbearing years (15-24), women are less viable than men. Such a reversal at these ages is not uncommon in peacetime in human groups in a poor state of health (Taeuber and Beal, '44). After 65 in Yap, the expectation of life is shorter for females than for males, perhaps because of neglect. At other ages, male mortality exceeds that of females—the usual finding in both human beings and lower animals (Hamilton, '48).

A phenomenon often seen in populations of Pacific islanders is their masculine sex ratio (Keesing, '52). This imbalance has been true of Yap at least throughout this century (Senft, '03; Nanyo Gunto, '32), and the ratio was 114 in 1948. In the absence of appreciable migration, such a pattern must reflect a highly masculine sex ratio at birth, a high mortality of females, or both. Table 4 shows the annual sex ratios of births for 1946 through 1951. The first three years have been extensively cross-checked. The last three are from government statistics and are therefore perhaps more likely to show under-representation of females.

TABLE 3

*Abridged Life Tables for Yap Males and Females, 1946-48*

AGE INTERVAL	NUMBER ENTERING EACH AGE	PROBABILITY OF DYING	NUMBER DYING	NUMBER LIVING AT EACH AGE	TOTAL YEARS REMAINING TO SURVIVORS	AVERAGE YEARS OF LIFE REMAINING TO SURVIVORS
$x$ to $x+n$	$l_x$	${}_nq_x$	${}_nd_x$	$L_x$	$T_x$	$e_x$
MALES						
0-	100,000	.0428	4,280	96,901	4,651,700	46.52
1-4	95,720	.0291	2,785	375,278	4,554,799	47.58
5-9	92,935	.0181	1,682	460,010	4,179,531	44.97
10-14	91,253	.0124	1,132	453,548	3,719,521	40.76
15-19	90,121	.0247	2,226	445,594	3,265,973	36.24
20-24	87,895	.0431	3,788	430,646	2,820,379	32.09
25-29	84,107	.0631	5,307	398,974	2,380,733	28.31
30-34	78,800	.0850	6,698	377,761	1,981,859	25.15
35-39	72,102	.1073	7,737	341,533	1,604,098	22.25
40-44	64,365	.1313	8,451	300,909	1,262,565	19.62
45-49	55,914	.1565	8,751	257,741	961,656	17.20
50-54	47,163	.1842	8,687	214,022	703,915	14.93
55-59	38,476	.2180	8,388	171,214	489,893	12.73
60-64	30,088	.2573	7,642	130,792	318,679	10.59
65-69	22,346	.3127	6,988	94,222	189,887	8.41
70-74	15,538	.4922	7,559	57,258	93,665	6.10
75-79	7,799	.5050	3,938	36,407*	36,407	4.67
80-	3,861		3,861			
FEMALES						
0-	100,000	.1413	14,130	88,870	4,460,886	44.61
1-4	85,870	.0210	1,803	338,944	4,372,016	50.91
5-9	84,067	.0183	1,538	416,041	4,033,072	47.97
10-14	82,529	.0134	1,106	410,380	3,617,031	43.83
15-19	81,423	.0484	3,941	397,975	3,206,651	39.38
20-24	77,482	.0584	4,525	376,083	2,808,676	36.25
25-29	72,957	.0532	3,881	354,934	2,432,593	33.34
30-34	69,076	.0551	3,806	335,947	2,077,659	30.08
35-39	65,270	.0654	4,269	315,881	1,741,712	26.68
40-44	61,001	.0785	4,789	293,305	1,425,831	23.37
45-49	56,212	.0992	5,576	267,411	1,132,526	20.15
50-54	50,636	.1221	6,183	237,989	865,115	17.08
55-59	44,453	.1543	6,859	205,356	627,126	14.11
60-64	37,594	.1949	7,327	169,898	421,770	11.22
65-69	30,267	.2654	8,033	131,936	251,872	8.32
70-74	22,234	.4772	10,610	84,872	119,936	5.39
75-79	11,624	.8260	9,601	34,964*	34,964	3.01
80-	2,023		2,023			

\* This is  ${}_xL_{75}$  and not  ${}_xL_{76}$ .

Table 4 indicates that a high sex ratio has been recorded for Yap, for unknown reasons. As shown in the life table, this initially high masculinity is increased by high female mortality in infancy, the early years of childbearing, and extreme old age, but is diminished by higher male mortality at most other ages.

TABLE 4

*Total Births and Sex Ratios at Birth, Yap, 1946-51*

YEAR	TOTAL BIRTHS	SEX RATIO	SOURCE
1946	70	133	Census by the authors
1947	82	160	
1948	66	89	
1949	71	109	Marshall ('53)
1950	97	131	
1951	100	127	

The combination of a highly masculine sex ratio at birth and a high female mortality in the first year of life is suggestive of female infanticide, but we found no direct ethnographic evidence of this practice and are not yet convinced that it explains these findings. Our observations of child care also revealed no relative neglect of infant girls.

The abrupt increase in the birth rate in Yap since the American occupation will be discussed later.

#### MALE ABSENTEEISM FROM YAP

Permanent immigration and emigration have had no appreciable effects on the depopulation. Only a handful of foreign immigrants now live among the Yapese, and some of these are undoubtedly transients. A few Yapese of both sexes have permanently emigrated to Palau, Truk, the Marianas, Ponape and even Japan. Temporary emigration of men from Yap, however, has been very prevalent in the past. Most of these men worked in the few commercially profitable German or Japanese enterprises in Micronesia, especially the phosphate mines at Angaur in the Palaus. These mines attracted laborers from many Micronesian islands. The wages and working conditions were good, and a large majority of the able-bodied Yap men gladly volunteered to work there. Some stayed abroad for many years, and repeatedly returned to their jobs after brief visits home.

Routine questions on the census schedules ascertained the number of trips abroad and the duration of each stay for every Yap male. A study was made of the men over 30 years of age by dividing them into those who had been abroad less than 5 years, and those who were away for 5 years or longer. Determinations of the average number of recognized progeny were then made, and a critical ratio calculated to test the significance of the difference observed. These findings are presented in table 5.

TABLE 5

*Duration of Male Absenteeism from Yap and Number of Recognized Progeny*

DURATION OF ABSENCE	N	NUMBER OF RECOGNIZED PROGENY		C. R.	p
		Mean	S. E.		
0-4.9 years	332	1.9 $\pm$ 0.2			
5.0 or more years	237	2.2 $\pm$ 0.2		1.1	0.27

Contrary to expectation, the men with the longer absences had a slightly larger number of recognized offspring, but this difference is not statistically significant. This test indicates that long absenteeism *per se* did not decrease the prolificacy of Yap men, probably because their employment abroad was typically discontinuous, with trips home often enough to sire some, at least, of the children considered by the community as being their own.

#### MALNUTRITION, PHYSICAL DETERIORATION, AND REPRODUCTION

An indirect but illuminating study of the reproductive potentials of the Yap islanders lies in their growth, diet, and body structure. In the past, a few physical anthropologists have dealt with these factors in evaluating the stability, florescence and deterioration of human societies and cultures. Hooton ('30), for example, found that the Indians of Pecos Pueblo, New Mexico, in successive generations showed facial shortening and enlarged occipital tori during their depopulation after the Spanish conquest. Angel ('44, '47) found that a better diet, relatively long life span, freedom from dental caries, and population increases accompanied the high points of cultural creativeness in the history of Greece. Correspondingly, the life span and population total decreased, and physical and dental deterioration set in, before the collapse of the Byzantine Empire.



Price ('39) investigated the malnutrition and physical deterioration of many formerly isolated human groups during their assimilation into the modern world economy. He found that this assimilation often involved an abandonment of the traditional local foods and the substitution of refined foreign products such as biscuits and sugar. The effects of such dietary innovations have been monotonously similar on human beings in much of the world, regardless of race, and include rampant dental caries, skeletal and facial malformations, difficult child-bearing, and perhaps even reduced fertility.

The evidence for physical deterioration as a part of the recent history of Yap might ideally have been studied by comparing early Yapese skeletal remains with the findings on the living population. Since it was impracticable to collect such remains from the village cemeteries, other sources of data were used instead. These sources included a series of aboriginal skulls from Guam, dating from just before or during the Spanish conquest in the 17th century, successive anthropometric samples of living Yapese adults dating from 1876 to 1948, and dental comparisons of the Yapese with other Pacific islanders.

If physical deterioration is related to a poor diet, the foods of Yap deserve consideration. Actually, the Yapese have been slow to adopt foreign foods. The islands support an abundance of edible plants which are seldom threatened except by occasional typhoons. These storms usually damage the plants, but seldom kill them. In recent generations, at least, no serious famines have contributed to the depopulation.

Like most other Pacific islanders, the Yapese chiefly live on root crops, fruits, fish and shellfish. The nutritional adequacy of such dietaries is uncertain, and may be highly variable from place to place. Alpert ('46) regards such diets in Micronesia as seriously deficient in proteins, calcium, iron, ascorbic acid, the B-complex vitamins, and calories. On the other hand, Price ('39) praises highly the quite similar aboriginal diets of Melanesia and Polynesia.

The most illuminating study of such diets is that of Hipsley and Langley ('53) in 4 New Guinea villages. The inhabitants of these villages probably have lower nutritive requirements than do Americans, because of their smaller bodies, tropical environment, less active mode of life, and the reduced specific dynamic action of their strongly vegetable diet. Hipsley and Langley believe that these people ingest enough calories, even though they generally do not become obese in middle age. They consume enough thiamin and ascorbic acid, but their protein and

calcium intakes are not so easy to evaluate. The nutritive value of vegetable protein is uncertain, but a genuine deficiency seems to occur in these dietaries. Calcium intake averages less than half of that specified in the standards for the United States calculated by the National Research Council, but in three villages with plentiful sunlight, very little rickets could be found in wrist roentgenograms of infants less than two years old.

In the absence of such data on the diet of the Yapese, we shall consider their gross physical state in its comparative, historical and developmental aspects, especially as related to their nutrition.

Our best evidence on the gross physical state of Micronesians in past centuries comes from old skeletal remains from Guam. Prior to the Spanish conquest, the Guamanians lived much as the Yapese do today, except that the Guamanian diet included somewhat more rice and seaweed. Since the dentition is an important indicator of nutritional status, a study by Leigh ('29) on the teeth of 106 old skulls from Guam gives us a valuable standard for evaluating modern Yap teeth.

Most of these skulls had an edge-to-edge occlusion of the incisors, although Leigh does not cite statistics, and only 15% showed any teeth out of line in the dental arches. The teeth were often discolored from betel chewing, but caries occurred in only 19 skulls, of which 11 showed senile lesions of the cementum. Many molars had faults and fissures where the cusps coalesced. In Guamanians who had died past the age of 30, teeth were often lost, especially in females, and the apparent reason for these losses was periodontoclasia.

TABLE 6  
*Incisor Occlusions and Crowding in Yap Adults*

SEX	AGES	N	UNDER- BITE	EDGE TO EDGE	SLIGHT OVER- BITE	PRO- NOUNCED OVERBITE	CROWDING OF TEETH		
							ABSENT	SLIGHT	PRO- NOUNCED
Male	20-49	343	2.0	45.2	43.2	9.6	42.7	46.0	11.3
Female	18-49	129	3.1	43.4	40.3	13.2	61.5	28.5	10.0

In most respects, the dentitions of the living Yapese are fairly similar. Table 6 illustrates the incisor occlusions in a series of adults. No significant sex difference was found, and although the edge-to-edge bite is the commonest condition, it seems to be somewhat less prevalent

than among the aboriginal Guamanians. Crowding is also somewhat more evident in Yap than in Guam. In Yap, it occurred mainly in the lower incisors and canines, such that a few teeth were slightly rotated or displaced. This condition was recorded as "slight" crowding. In "pronounced" crowding, all of the lower front teeth and premolars were considerably displaced or rotated, and in many cases, the upper front teeth were likewise out of alignment. These cases, however, were almost never as serious as one routinely sees in an orthodontic clinic, and were not accompanied by gross asymmetries of the nasal septum nor mouth breathing. The women showed significantly less crowding than the men except in the "pronounced" category.

As a result of their similar habit of betel chewing, the Guamanians and Yapese usually exhibited brownish, discolored teeth. There is no evidence, however, that this habit causes dental caries. Table 7 indicates that the younger Yap men have slightly more decayed teeth than the women. This difference may stem from the consumption of foreign foods by some of these men during their periods of work in foreign settlements—whether abroad or in Yap itself. In the older Yapese, the women have more caries. In general, the teeth of these people are fairly resistant to decay, but may be more carious than those of the ancient Guamanians.

TABLE 7

*Percentages of Carious Teeth in Yap Adults*

AGES	N Males	% CARIOUS Teeth	N Females	% CARIOUS Teeth
15-19	38	2.48	25	2.09
20-24	74	1.71	23	0.73
25-29	82	1.88	33	2.05
30-34	83	2.00	19	2.74
35-39	67	1.33	21	1.59
40-44	25	2.08	12	2.92
45-49	14	1.58	9	2.34

Other evidence on the low incidence of caries in Yap can be seen in table 8, in which data are combined from two investigators who studied this disease in Micronesian school children. Kuwahara ('41) worked out the incidence of caries in Palau, Truk, Ponape and Jaluit, and Hartmann ('47) studied two groups on Yap. Hartmann's two series

included a group of Yap native children, and also a sample of highly acculturated Chamorro children who lived at that time in Colonia, Yap. The diets of these two groups differed mainly in that the Chamorros ate more bread and rice. The statistics from all these groups show that the Yapese native children were the most caries-resistant of any. The lack of relationship between betel chewing and caries in these children can be seen in the fact that outside of the Chamorros and Yapese, only the Palauans chew betel.

TABLE 8

*Percentages of Carious Teeth in Micronesian School Children*

Kuwahara ('41)		Hartmann ('47)	
Ponape	57.67	Chamorros (Colonia, Yap)	10.28
Jaluit	42.83	Yapese	5.84
Palau	38.57		
Truk	13.16		

Table 9 shows that the loss of teeth in Yap is not unlike that of the prehistoric Guamanians, and sets in during the middle thirties. A similar rate of loss has also been found in three New Guinea villages on substantially aboriginal diets (Sinclair et al., '53). In the Yapese, the standard deviations of the numbers of remaining teeth increase after the thirties, since some individuals lose teeth faster than others in middle age. During this period of loss, the teeth become non-vital,

TABLE 9

*Mean Number of Teeth Present in Yap Adults*

AGES	N Males	NUMBER OF TEETH		N Females	NUMBER OF TEETH	
		Mean	$\sigma$		Mean	$\sigma$
15-19	38	28.6	1.3	25	28.7	1.1
20-24	74	30.1	1.7	23	29.9	1.7
25-29	82	31.2	1.4	33	31.1	1.5
30-34	83	31.3	1.5	19	30.8	1.5
35-39	67	30.4	4.3	21	30.0	2.7
40-44	25	26.9	8.2	12	28.6	6.0
45-49	14	26.1	8.2	9	28.4	4.7
50-54	8	22.3	11.6	9	26.4	10.1



more and more loose, and finally drop out. Elderly Yap informants said that the actual loss of a tooth was seldom painful. These symptoms are probably indicative of periodontoclasia. The possible relationship of betel chewing to this loss of teeth is unknown.

The emergence of the third molar teeth in Yap males, as shown in table 9 and in other data as well, tends to be late. In a series of Harvard undergraduates whose ages at third molar emergence have kindly been supplied by Dr. Clark W. Heath, of the Harvard Study of Adult Development, the median age of emergence was about 20 years. In Yap males it was 22. These teeth are slightly less apt to emerge in Yap females than in males and, as a result, up to the age of 39, the women have fewer visible teeth than the men. After this age, the males lose teeth faster than the females, unlike these rates in the Guamanian crania cited previously. In Yap, the years of lactation and pregnancy are not a time when women lose teeth faster than men. In the much more carious teeth of the people of Puerto Rico, however, Thieme ('53) found that between the ages of 20 and 45 years, the women lost an average of 0.58 teeth per year, while the men lost only 0.29.

TABLE 10

*Successive Anthropometric Series of Yap Adults*

AUTHOR	DATE OF MEASUREMENTS	N	STATURE RANGE	STATURE MEAN	NOSE BREADTH	HEAD LENGTH	HEAD BREADTH
<b>Males</b>							
Miklucho-Maclay	1876	30	150-169	—	—	—	—
Hambruch	1906	7	—	164	41	188	146
Hirako	1915	8	159-171	164	—	191	150
Hasebe	1927	46	—	160	42	189	146
Arai	1939	189	—	162	44	189	148
Hunt	1948	347	146-178	161	42	189	150
<b>Females</b>							
Miklucho-Maclay	1876	11	136-158	—	—	—	—
Arai	1939	75	—	149	39	179	141
Hunt	1948	143	135-164	150	37	179	143

From 1876 to 1948, 6 investigators have measured series of living Yap adults, and their findings are presented in table 10. If these data suggested any recent systematic shrinkage in Yapese bodily dimensions, one might argue that this trend was indicative of deteriorating nutriture.

No such decrease was found. In spite of the smallness of some of these samples, table 10 indicates that the Yapese today are much the same size as their ancestors were more than 70 years ago. This metrical stability is quite unlike the increase in stature during recent generations in many civilized populations (Bowles, '32), and seems to be only one of a great many manifestations of dietary and cultural conservatism still prevalent in Yap.

Alpert ('46) found a number of characteristics in many Micronesians which he attributed to dietary deficiencies. He did not examine any Yapese for these signs, however. Included in his list were vascularity and thickness of the conjunctiva, redness of the tongue with a fissuring of the surface, atrophy and fusion of the filiform papillae, and hypertrophy of the fungiform papillae. A few Micronesians showed an actual edema of the tongue. Alpert believed that these symptoms resulted from deficiencies of the B vitamins, especially niacin. A prevalent recession and hypertrophy of the gums he attributed to a deficiency of ascorbic acid.

In the medical survey conducted by the *Whidbey*, McNair et al. ('49) observed conjunctivitis in about 10% of the Yapese. Other gross nutritional deficiencies were not apparent, and these authors think that only subclinical cases exist in Yap.

Examinations by Hunt during the Harvard anthropometric survey revealed many cases of fissuring of the tongue. Sloughing and bleeding of the gingival and oral mucosa also appeared, but in each case the islander said that he had accidentally burned his mouth from putting too much lime in his betel quid. This betel irritation makes the identification of avitaminoses uncertain. Since the Yapese eat numerous oranges and pineapples from their own islands, it is not too likely that they are deficient in ascorbic acid.

Alpert also mentions the slow maturation of the Micronesians as evidence of their inadequate diet. Children in Yap certainly mature less rapidly than recent series of American children. For 1948, the median age of menarche in Yap girls was determined from the number of individuals at each age from 10 to 17 years who had or had not entered the postmenarcheal age grade, as noted in the census. This median age was 14.3 years, which is a year or more older than mean menarcheal ages found in most recent American growth studies (Stuart, '46). Smoothed mean statures for adults at different ages indicate that full adult stature is reached at about 26-27 years in Yap men, and 20-24

years in women. For males, full stature is reached some 2 years later than in American Whites (Randall, '49), as is the emergence of their third molar teeth.

The interpretation of this slow maturation is difficult. Hipsley and Langley ('53) think that diets deficient in protein in New Guinea slow down the growth of the people there. Mills ('42) believes that hot and humid tropical climates retard human growth. Craig and Faust ('45) observe that children with severe infestations of intestinal parasites mature slowly. Some or all of these explanations may apply to Yap.

Childbearing in Yap is usually easy, and puerperal sepsis is rare, even after deliveries by island midwives (McNair et al., '49). After being delivered in the hospital, a Yap woman may walk off, carrying her newborn child.

In general, the caloric nutriture of Yapese adults seems adequate, but they are among the growing list of Pacific island peoples in whom obesity in middle age has been observed to be rare (Keesing, '52; Keys and Brožek, '53; Hipsley and Langley, '53).

In general, the preceding data do not indicate any obvious or severe malnutrition in Yap. Depopulation can evidently occur in a human group with little or no concomitant physical deterioration.

#### INTESTINAL PARASITES

Another phenomenon of possible relevance to the depopulation is the great prevalence of intestinal parasites in the Yapese. Fujii ('34) found that 98.9% of a large Yap series harbored the nematode *Trichostrongylus*, 50.3% had hookworm (ancylostomiasis), 33.2% *Ascaris* (roundworms), and 3.2% the pinworm *Enterobius* (*Oxyuris*). An unpublished study by a medical officer on Yap, Dr. E. C. Cowart, showed that 97% of a sizeable sample of Yapese harbored at least two of these species of parasites in 1948. When the American medical officers tried to eradicate these infestations by treatments with hexyl-resorcinol crystoids, practically all of a group of Yapese became re-infected in a few weeks. These infestations probably result from Yapese habits of defecating in the bush, walking barefoot and sitting on polluted ground, eating raw food and drinking unboiled water.

The Whidbey survey of stool specimens from 1,294 Yapese revealed that 83% showed parasitic infestations. *Trichostrongylus* and *Ancylostoma* were the commonest species found, as in the Japanese studies, and other types were only sporadically present.

The possible relevance of these infestations to the depopulation may be inferred from data in textbooks of parasitology such as Craig and Faust ('45). Evidently *Ancylostoma* and *Enterobius* are both known to impair human reproduction. In some cases, *Ancylostoma* may cause impotence in men and stillbirths in women. *Enterobius* may even infest the female genital tract and enter the abdominal cavity by way of the uterine tubes.

Although intestinal parasites may have slightly depressed the birth rate in Yap, it is also true that seriously infested peoples such as the Javanese and Egyptians are among the most rapidly increasing populations in the world.

#### REPRODUCTIVE PATHOLOGIES AND ABORTIONS

The most intensive survey of the diseases of the genitals in Yapese of both sexes was carried out by Fujii ('34). American physicians so far have had more limited experience with this problem. For example, members of the *Whidbey* survey made urogenital examinations of the men only (McNair et al., '49).

Both surveys found practically no syphilis in Yap. Fujii seldom saw indurated chancres, and McNair et al. ('49) report that "no case of primary chancre was found, nor were secondary skin manifestations found among the men or women." Fujii states that chancroids are also rare.

In spite of the considerable experience of many physicians in Yap, the incidence of gonorrhea is still in doubt, and we do not know whether it has changed during the American occupation. Fujii ('34) thought that this disease was the chief cause of the former low birth rate, and attempted to discover its incidence by both clinical and microscopic examinations of thousands of Yapese of both sexes. In 1,102 women, 42.8% had gonorrheal vaginitis and endometritis, and Fujii suspected that inflammations of the tubes and ovaries were also prevalent. American physicians have often seen mucus blocks, cervicitis, and yellow exudate from the vagina in Yap women. Fujii also states that in 1,252 Yap males aged 8 to 60, 46.8% showed epididymitis, prostatitis or urethritis, but gonorrhea was positively diagnosed in only 24.8% of this entire male group. In all, Fujii believed that 784 Yapese of both sexes whom he examined were infected with gonorrhea. He treated 88 of these cases, 72 of whom were women. Subsequent to therapy, 15 of these women became pregnant for the first time.



In September, 1945, the United States Navy occupied Yap. Monthly reports sent from Yap to the Department of the Navy indicate that a dispensary was set up, and in January, 1946, 754 adult islanders were treated with arsenicals for yaws. An unspecified number of children were given 400,000 units of penicillin apiece for this disease. In February, 1946, 629 cases of yaws were treated. This program of mass therapy was so successful that only a few individuals needed further treatment. At the time of the *Whidbey* survey in 1948, no active "raspberry-like" lesions of yaws were seen, although both "tissue-paper-like" and keloid scars of former yaws were quite prevalent.

In startling contrast to the evidence of Fujii, the *Whidbey* survey of diseases of the male genitalia disclosed only 4 men with gonococcic urethritis, and one with nonspecific urethritis. We are still ignorant of whether old chronic gonorrhea in a form unrecognized by the American physicians is actually still widespread in Yap, or whether the mass treatment of yaws has somehow reduced the incidence of genital pathologies in the Yapese.

Before the American regime, Yap women used spongy wads of plant fibers to absorb the menses. These wads were sometimes kept in the vaginal canal. More recently, the women have begun to buy American sanitary napkins, and this practice may have alleviated some of their vaginitis.

According to Schwidetzky ('50), the percentages of married women in various human groups who have ever borne children range from about 75 to 95%. The converse percentages of infertile married women would be 5 to 25%. Since nearly all mature Yap women have had some marital experience, data on their infertility are worth comparing with these percentages. Within the age range of 26 to 50 years, Fujii ('34) found that 30.8% of 622 women claimed never to have been pregnant, and this incidence from 424 such women in our census was 34.4%.

In the 1,417 Yap births recorded from 1917 to 1929 by Fujii ('34), 5.9% ended in miscarriage or stillbirth. For 1,622 progeny reported by the fertile women in our census, this incidence was 5.2%. Comparable rates for Fiji in 1890 and 1891 were 5.22% and 6.13% (Krzywicki, '34), and for rural "colored" people in the U. S. Birth Registration area from 1922 to 1936, this rate was 6.37% (Strandskov and Roth, '49). Yap therefore resembles these other unhealthy groups in reproductive wastage, but since stillbirth rates are notoriously inaccurate, comparisons are risky.

If a Yap woman does become pregnant, she will not always carry her child voluntarily until term. She may deliberately induce an abortion by expedients such as drinking concentrated salt water and lacerating the cervix with a wad of leaves. Although an effort was made in our census to account for every pregnancy of every living Yap female, these women knew that both foreigners and Yap men disapprove of deliberate abortions. Some of the women who falsely reported no pregnancies to both Fujii and ourselves may actually have become sterile because of this practice, or at least afflicted with cervicitis. As in most other statistics on stillbirths, concealment of deliberate abortions probably introduces an unknown amount of error into the stillbirth rates for Yap of both Fujii and ourselves.

We believe that pathologies of the genitalia in Yap—whether venereal disease or not—considerably depressed the crude birth rate before 1946. Improvements in these conditions may have occurred since then, but are probably not the only reasons why the crude birth rate has recently doubled.

#### COPULATION, CONTRACEPTION AND FERTILITY

Several additional factors seem to have limited the numbers and survival of the progeny produced by Yap parents. A brief account of the individual life cycle and sexual activities of the Yap people will highlight some of these reproductive limitations.

The Yap child typically passes from a secure and well-fed infancy into a long period when he is virtually free from responsibility. Adolescents of both sexes are not encouraged to do serious work, and soon embark on premarital, somewhat secret, love affairs. Love trysting in Yap includes witty conversation, romantic songs, betel sharing, gift exchanges, and the drinking of fermented coconut sap (toddy). These encounters usually take place out of doors, in secluded parts of the village. The partners often engage in prolonged embraces and slow friction of the penis and clitoris, during which the male ejaculation occurs within or outside of the vagina. A married man is unwilling to perform this act with his wife for fear of causing her to insist on it too often, thereby making him too debilitated to work. Ordinary sexual intercourse, however, is indulged in by both unwed and married couples.

In late adolescence and younger adult years, couples will usually live together openly in marriage, generally in patrilocal residence but in a separate dwelling. These unions are not necessarily permanent, espe-

cially if the wife produces no children. The married partners typically show little overt affection for each other. Instead, both may engage in surreptitious extramarital sexual affairs. Yap adults usually go through more than one such temporary marriage, and little or no social pressure is customarily exerted on couples to stay married unless children are born. Such tentative matings usually take place before the age of 30 years, when the partners are not yet expected to have acquired the responsible habits of maturity.

Until recently, extramarital copulation for the young men also took place in their club houses. Young female entertainers were kept there as honored and respected sexual partners of the club members, and played a role comparable to that of Japanese *geisha*.

The aboriginal Yap islanders were among the many Oceanic peoples who apparently believed that sexual intercourse does not cause pregnancy, and that children result only from the intervention of supernatural beings. This opinion is still expressed by some Yapese, but does not lead to unrestrained copulation at any time or place. Coitus is theoretically forbidden when a man is fishing or constructing a canoe, a house or a road. If he becomes an important religious specialist, he is expected to remain continent for life. Continence is also enjoined on participants in sea voyages, ceremonials, and mourning for the dead. A woman should not copulate during menstruation, pregnancy, nor from her confinement until her offspring can walk and speak.

A small survey of the recall of recent sexual intercourse was carried out, using 16 adult informants from Rumung, an isolated island at the northern tip of Yap. This survey showed considerable awareness of many of these coital restrictions. It was made at a time when most of the men were harvesting trochus shells from the sea, and were therefore under the temporary ban on coitus which is connected with fishing. Although the coital frequencies revealed in this survey may be lower than usual, only 4 of the 16 informants admitted to copulation within the previous 10-15 days.

In considering this evidence, it is noteworthy that most samples of males in the U. S. aged 16-40 years admit to an average coital frequency of at least once a week (Kinsey et al., '48). The frequency reported by the Yapese is evidently much lower, but may be unrepresentatively so because of the trochus season, the small sample, or the islanders' own attitudes toward sexual intercourse. The usual jibe at a man who is weak or unwilling to work is that he has been copulating "too much."



Many Yap men said that "too much" copulation made them incapacitated or ill. Coital excesses and violations of other prohibitions against sexual indulgences lead to the death of the transgressor in several Yap folk tales, generally from fish bites or supernatural vengeance. "Too much" intercourse is defined as something over two or three copulations per month. This sentiment against "frequent" coitus makes it quite possible that the informants in our survey minimized their erotic revelations out of a reluctance to admit that they had copulated "too much."

When unmarried couples produce orgasms by friction of the penis and clitoris, this activity may reduce the likelihood of conception. Other, more deliberate, contraceptive techniques are known but seldom used, whether *coitus interruptus*, condoms, mechanical obstruction of the cervix, or douches of concentrated salt water after copulation. These measures seem to have been unimportant factors in the depopulation.

Recent evidence (Farris, '50) indicates that a woman usually tends to ovulate at about the middle of her monthly cycle, and is probably capable of conception for several hours afterwards. The timing of coitus within this cycle is therefore a significant aspect of human reproduction. In Yap, a woman is expected to remain continent during menstruation, when she is secluded in a menstrual area. During the rest of her cycle, however, the Yap people express no particular preference for the time of copulation.

During the Japanese regime, several Yap informants stated that Japanese physicians gave them lectures on how to have more children. These instructions were that couples should have intercourse during the week just before or just after menstruation. This plan was probably based on the obsolete and erroneous premise that ovulation and conception are most likely to occur at this time. If any of the Yapese followed this advice, they may have been reproductively frustrated. The degree of conformity to this plan in Yap, however, seems not to have been strict. In our opinion, it was not a major depressant of the birth rate during the Japanese period.

Recent studies of the fertility of American Whites (Farris, '50) do not suggest any simple relationship between coital frequencies and conception rates in human populations. Farris found that the number of spermatozoa in an average ejaculation of semen is maximal if the donor has not ejaculated during the previous 5 days. As the preceding interval of continence decreases below 5 days, the sperm count decreases, until at three days or less, a man with an average output of spermatozoa



generally produces too few of them at a coital orgasm to be likely to impregnate his partner. On the average, a woman should therefore be most likely to conceive at a given copulation if her partner has not ejaculated during the preceding 4 days or more.

Extrapolating these findings to the fertility of human populations, it is likely that with intervals between copulations conforming to a normal curve, two societies might have identical conception rates where one group copulated at a mean interval of much less than 5 days, while the other's interval was considerably longer.

In Yap, if the low coital rate also reflects a low total frequency of male ejaculations, most men at coitus would produce a maximum number of spermatozoa. The sexual license of the younger Yapese might also allow an unusually fecund man to impregnate more than one woman. Other features of these same coital patterns, however, may depress fertility in Yap. The spread of venereal diseases through Yapese promiscuity is an unproved but possible depressant. The instability of marriages of childless women is another. According to Pearl ('40), a woman is apt to be most fertile late in her teens or soon afterward. At these ages, many Yap women circulate from one husband to the next, and their coital experiences may therefore be episodic and irregular.

Still another limitation on the number of children in Yap stems from the reluctance of many women to have large families. A mother's burdens of gardening and cooking are considerably increased when her older children come to belong to more than one age grade. These burdens arise because each grade must be fed with rations from its own separate garden, as a part of the emphasis on rank, social distance, and separation of the sexes in Yap. Many woman therefore openly state that they hope to have only a few children in order to save themselves from too much work.

#### THE RECENT INCREASE IN THE YAP POPULATION

In retrospect, we shall probably never know whether the Yapese were potentially capable of a high birth rate during the depopulation. Judging from their diseases and high mortality, their burden of ill-health must have been heavy. Since the American occupation, yaws have largely disappeared, and mortality has greatly decreased. When such improvements occur very rapidly in a human group, increased fertility might reasonably be expected, even though its causes are not well understood.

Although space does not permit a full treatment of recent demographic statistics or forecasts for Yap, the gross reproduction rate for 1946-48 was 1.593, and the net reproduction rate was 1.135. The net rate falls below the gross rate by 28.8%, and this deficit indicates the persistence of a high mortality among young females, as previously shown in the life tables. The true rate of natural increase ( $r$ ) per year is 4.79 per thousand. In an approximate generation (26.69 years), if age-specific fertility and mortality remained at the levels of 1946-48, the breeding population of females would increase by 13.5%. Since 1948, however, the crude birth rate has continued to rise, and mortality has still further diminished. In 1946-48, an average of 32 females were born per year. In 1949-51, however, the average was 41 girls born per year, so that by now the female Yapese are increasing still more rapidly than before. The highly masculine sex ratio at birth, and relatively low male mortality, make the increase of males still more probable and rapid in the next generation.

From the Spanish period until 1948, a small community of Chamorros from the Marianas lived on Yap near Colonia. This group has since been resettled on Tinian. In 1946, they had a crude birth rate of about 30 per thousand, and were probably quite prolific during the Japanese period as well. The Yapese living near them have slightly straighter hair than the inhabitants of more remote parts of the islands, which suggests some Chamorro admixture, but practically no Yap children in 1948 showed evidence of mixture with Japanese or Whites. Furthermore, the Yap birth rate in 1951 was still high, long after the Chamorros had left. We therefore attribute substantially all of the recent increase in the Yapese birth rate to their own sexual activities.

As the control of disease in Yap has improved, several social and cultural changes have also helped to enhance the fertility of the islanders. One such change is that few young men are now working outside of their home villages, either in Colonia or abroad. Instead, they are at home enough so that they probably have more uninterrupted sexual access to young Yap women than in the past.

A rumor was current among the Yapese in 1948 that a secret meeting on the depopulation was held by the chiefs and religious leaders in 1946. These men supposedly decided that most of the former taboos on coitus should be discontinued. Even at the time of our coital survey in 1948, however, these regulations were still invoked as explanations for alleged sexual abstinence.

The Yapese are now unquestionably undergoing considerable acculturation toward the American way of life, of which this rumor is symptomatic. Although material objects of Japanese or American origin are more numerous near Colonia, the extent of acculturation in values and behavior is not very different in the various parts of Yap.

Two other demographically important aspects of acculturation have been a relaxation of the interdining restrictions among the various age grades and between the sexes, and improvement in feminine hygiene. As more family members feel free to eat together, the domestic chores of a mother become easier, and her desire for children may increase. When a woman wants children, she may be less inclined to end her pregnancies by deliberate abortions. At menstruation, she is beginning to use sanitary napkins rather than local plants. These improvements probably have helped to alleviate female infertility and increase the birth rate.

With a higher birth rate, an increase in marital stability can also be expected, since fertile couples usually stay married for life. Stable marriages, furthermore, should increase the likelihood of additional children to be born, so that the present fairly high birth rate is maintained.

The future survival of the Yap people apparently depends on improvements in health, sanitation and marital stability, and on maintaining a high morale. If these conditions deteriorate, the population may well resume its interrupted decline. Otherwise it may continue its present moderate increase.

#### SUMMARY

Over a century ago, the Micronesians of Yap began to decrease in numbers. The first census of this group, in 1899, showed a total of 7,808 Yapese. In 1946, there were only 2,582. Subsequently their numbers have slightly increased.

An increase in mortality, chiefly as a result of severe infectious diseases, probably started the decline, and even after several decades of foreign rule, the crude death rate was still high. From 1917 to 1930, the crude death rate was about 40 per thousand. Poor health conditions prevailed in Yap, including 5 known epidemics and widespread yaws and pulmonary tuberculosis. The crude birth rate for 1917-30 was only about 15 per thousand, so that the depopulation continued unabated.

This low birth rate seems not to be explained by the absence of men

from Yap. Although most Yap men spent years as laborers in other parts of Micronesia, the men absent for more than 5 years had as many recognized progeny as those away for a shorter period. The absentees were seldom continuously abroad, and usually visited Yap often enough to sire some, at least, of the children attributed to them.

The low birth rate of the Yapese in the past may partially be explained by some of the pathologies of their genitalia. In the early 1930's, Fujii conducted medical examinations of thousands of Yapese, and found widespread genital infections which he regarded as gonorrhea. Under the American administration, mass treatments with arsenicals and penicillin have virtually eliminated yaws, but whether the genital diseases of the Yapese are less severe now than previously is unknown. A recent American medical inspection of the genitalia of most of the men revealed practically no gonorrhea, but whether old chronic infections were overlooked during this survey is uncertain. Another minor depressant of fertility may be the presence of intestinal parasites in nearly all Yapese.

Despite the infectious diseases of these islanders, they were and are otherwise well off physically. They eat few foreign foods. Caries and malocclusions of the teeth are rare. The children mature slowly, perhaps because of the tropical climate, intestinal parasites, or even perhaps a subclinical protein deficiency. Puerperal sepsis and other obstetrical difficulties are uncommon.

The much reduced birth rate during the Japanese period may in part have resulted from the poor health and debility of the islanders, but numerous cultural patterns in Yap seem to have limited fertility. In the culture of Yap, rank and prestige are greatly emphasized, so that men and women eat apart, and even individuals of different age grades also eat separate food. The inconvenience of this kind of house-keeping within the family leads many women to hope for only a few children. During the Japanese regime, the difficulty of raising a family when the husband was often abroad may also have minimized the desire for children. At that time, pregnancies may often have been terminated by deliberate abortions. Menstrual hygiene was also unsanitary. Along with infectious diseases in both sexes, these conditions seem to have contributed to the claim of about one third of the women aged 26-50 that they had never been pregnant.

Since the arrival of the Americans, the crude birth rate has doubled and the crude death rate halved. Health has improved, and several



social and cultural changes seem to have helped to raise fertility. Few young men are now outside of their home villages. Coital taboos are probably relaxing. More family members are eating together than previously, so that housekeeping is easier, and the mother's desire for children is probably increasing. Fewer abortions and better menstrual hygiene may be enhancing female fertility. As more children are born, marriages are becoming more stable, so that the likelihood of additional childbearing increases. With improved health and sanitation and a high morale, the population will probably continue to show a moderate increase.

## LITERATURE CITED

- ALPERT, E. 1946 Nutrition and Diet. U. S. Commercial Company Survey of Micronesia, 1 $\frac{1}{2}$ . 23 pp.
- ANGEL, J. L. 1944 Greek teeth, ancient and modern. *Human Biol.* 14: 283-297.
- 1947 The length of life in ancient Greece. *J. Gerontol.* 2: 18-24.
- ANNUAL REPORT OF IMPERIAL JAPANESE GOVERNMENT TO LEAGUE OF NATIONS MANDATES COMMISSION, 1936.
- ARAI, S. 1953 Anthropometric research on the Micronesians. *Proc. 7th Pacific Science Congress.* 218-220.
- BOWLES, G. T. 1932 New Types of Old Americans at Harvard. Harvard Univ. Press, Cambridge, Massachusetts.
- CRAIG, C. F., AND E. C. FAUST 1945 Clinical Parasitology. 4th Ed. Lea and Febiger, Philadelphia.
- DUBLIN, L. J., A. J. LOTKA, AND M. SPIEGELMAN 1949 Length of Life. The Ronald Press, New York.
- FARRIS, E. J. 1950 Human Fertility and Problems of the Male. Author's Press, White Plains, N. Y.
- FUJII, T. 1934 Endemic diseases in the Caroline Islands (in Japanese). Collection of Medical Essays 3. South Seas Government Office, Tokyo.
- GREVILLE, T. N. E. 1943 Short methods of constructing abridged life tables. *Rec. Am. Institute of Actuaries* 32: 29-42.
- HAMBRUCH, P. 1909 Beiträge zur Somatologie von Madagaskar, Indonesien, Bismarck-Archipel und Mikronesien. Forschungsreise S. M. S. Planet, 1906-1907, Berlin.
- HAMILTON, J. B. 1948 The role of testicular secretions as indicated by the effects of castration in man and by studies of pathological conditions and short lifespan associated with maleness. *Proc. Laurentian Hormone Conf.* 3: 257-322.
- HARTMANN, F. W. 1947 Prevalence of dental caries in two groups of children in Micronesia. Report to the National Research Council, sponsored by Univ. of Hawaii Pacific Research Committee.
- HASEBE, K. 1938 The natives of the South Seas Archipelago (in Japanese). *Jinruigaku Senshigaku Koza (Lectures in Anthropology and Prehistory).* 1.

- HIPSLEY, E. AND D. LANGLEY 1953 A nutritional survey of New Guinea natives. Proc. 7th Pacific Science Congress. 418-427.
- HIRAKO, G. 1918 An anthropometrical study of the Micronesians. Proc. 3rd Pacific Science Congress, 2: 2399-2404.
- HOOTON, E. A. 1930 The Indians of Pecos Pueblo. Papers of the Southwestern Expedition 4, Phillips Academy, Andover. Yale Univ. Press, New Haven.
- HUNT, E. E., JR. 1950 A view of somatology and serology in Micronesia. Am. J. Phys. Anthropol., n. s. 8: 157-184.
- HUNT, E. E., JR., N. R. KIDDER, D. M. SCHNEIDER, AND W. D. STEVENS 1949 The Micronesians of Yap and their Depopulation. Mimeographed report to the Pacific Science Board, National Research Council, from the Peabody Museum, Harvard University, Cambridge, Massachusetts.
- KEESING, F. M. 1952 Research opportunities in New Guinea. Southw. J. Anthropol. 8: 109-133.
- KEYS, A., AND J. BROZEK 1953 Body fat in adult man. Physiol. Rev. 33: 245-325.
- KINSEY, A. C., W. D. POMEROY, AND C. E. MARTIN 1948 Sexual Behavior in the Human Male. W. B. Saunders and Co., Philadelphia.
- KRZYWICKI, L. 1934 Primitive Society and its Vital Statistics. Macmillan and Co., Ltd., London.
- KUWAHARA, S. 1941 Investigation upon the decayed teeth among school children of Micronesia. Kagaku Nanyo (Science of the South Seas) 4: 34-52.
- LEIGH, R. W. 1929 Dental morphology and pathology of prehistoric Guam. Memoirs of the B. P. Bishop Museum, 11: 257-273.
- MARSHALL, H. L. 1953 Personal communication.
- MATSUMURA, A. 1918 Contributions to the ethnography of Micronesia. J. Coll. Sci. Imperial Univ. of Tokyo, 40: 1-174.
- McNAIR, P. K., R. R. GARISON, J. H. GILPIN, ET. AL. 1949 Report of a Medical Survey of the Yap District of the Western Caroline Islands of the Trust Territory of the Pacific Islands. Hosp. Corps Quarterly, 22(4): 5-19.
- MIKLUCHO-MACLAY, N. VON 1878 Anthropologische Notizen gesammelt auf einer Reise in West-Mikronesien und Nord-Melanesien im Jahre 1876. Verh. der Berliner Gesellschaft für Anthropol., Ethnologie und Urgeschichte: 102-109.
- MILLS, C. A. 1942 Climatic effects on growth and development with particular reference to the effects of tropical residence. Am. Anthropologist, 44: 1-13.
- MURDOCK, G. P. 1948A New light on the peoples of Micronesia. Science, N. S., 108: 423-425.
- 1948B Anthropology in Micronesia. Trans. N. Y. Academy of Science, Series II, 11: 409-416.
- NANYO GUNTO (SOUTH SEAS ARCHIPELAGO) 1932 Published by Tosei at Chosa Sho, Tokyo. Vol. 2 (in Japanese).
- PEARL, R. 1940 Pregnancy rates and coitus rates. Human Biol., 12: 545-548.
- PRICE, WESTON A. 1939 Nutrition and Physical Degeneration. George Routledge and Sons, Ltd., New York.
- PRICE, WILLARD 1936 Hypodermic for a dying race. Asia, 36: 523-526.

- RANDALL, F. E. 1949 Age changes in young adult army males. *Human Biol.*, 21: 187-198.
- REED, L. J., AND M. MERRELL 1939 A short method for constructing an abridged life table. *Am. J. Hygiene*, 30: 33-62.
- REPORT ON THE ADMINISTRATION OF THE TRUST TERRITORY OF THE PACIFIC ISLANDS BY THE UNITED STATES TO THE UNITED NATIONS 1952.
- SCHNEIDER, D. M. 1953 Yap kinship terminology and kin groups. *Am. Anthrop.* 55: 215-236.
- SCHWIDETZKY, I. 1950 *Grundzüge der Völkerbiologie*. Ferdinand Enke Verlag, Stuttgart.
- SENEFT, A. 1903 *Ethnologische Beiträge über die Karolineninsel Yap*. Petermanns Mitteilungen, 49: 49-60, 83-87.
- SINCLAIR, B. Y., D. A. CAMERON, AND N. E. GOLDSWORTHY 1953 Some aspects of dental caries among native peoples of Papua-New Guinea and European inhabitants of Australia. *Proc. 7th Pacific Science Congress*: 434-450.
- STRANDSKOV, H. H., AND J. A. ROTH 1949 A comparison of rural and urban birth sex ratios for the total, the "White," and the "Colored" U. S. populations. *Am. J. Phys. Anthrop.*, n. s. 7: 9-100.
- STUART, H. C. 1946 Normal growth and development in adolescence. *New Engl. J. Med.* 234: 666-672.
- TAEUBER, I. B., AND E. G. BEAL 1944 The dynamics of population in Japan. In *Demographic Studies of Selected Areas of Rapid Growth*, *Proc. Round Table on Population Problems*. Milbank Memorial Fund, New York.
- THIEME, F. P. 1953 Variations in caries frequency by sex and site. *Proc. 22nd Annual Meetings, Am. Assoc. Phys. Anthrop.*, *Am. J. Phys. Anthrop.*, n. s. 11: 251.
- YANAIHARA, T. 1939 *Pacific Islands under Japanese Mandate*. Kelly and Walsh, Ltd., Shanghai.





## THE QUESTION OF PHYSICAL SELECTION OF MEXICAN MIGRANTS TO THE U. S. A.

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IN a recent comparison of the physique of Mexican migrants and sedentes, I presented data bearing on the question of selective migration (Lasker, '52). After their return to their home town in Mexico, those male emigrants who had first left when already mature did not differ significantly from sedentes. Under the assumptions made in that study, it appears that environmental growth factors rather than selective emigration are responsible for differences between sedentes and emigrants who had left when still immature. At least, insofar as the physical characteristics under study are concerned, there was no sign of physical correlates of self-selection or selection by others among emigrants who had returned to Paracho, Michoacán, prior to 1948. As a matter of fact, in the generation reaching adulthood during the period between the Madero revolution (1910) and the end of World War II (1945), the young men of Paracho normally looked forward to periods of temporary labor in the United States.

Such semi-permanent migration used to be typical. Over the years, however, the opportunities for such migration have been decreasing. During World War II the governments of the United States and Mexico agreed to a system of labor contracting and the prohibition of the admission of individual job-seekers. As long as the war continued, however, there was an acute labor shortage in the United States, and contract laborers, hired in Mexico, were insufficient in number to meet the demand north of the border. There was, therefore, little selection and most Mexican men who wished to go to the United States to work were able to get a contract to do so.

After the war (and until January, 1954), on the other hand, the



United States tried to enforce the policy of limiting the number of *braceros*, laborers admitted for temporary residence, and of excluding non-contractual migrants. Agents of the United States Department of Agriculture, acting for American employers, have not only recruited but actively selected the contract laborers in Mexico. Numerous men in Paracho who wished to go to the United States have travelled to San Pedro Tlaquepaque, Jalisco, to be interviewed. Some received contracts and went to the United States but many others were rejected and returned home. It seemed worth while to investigate whether, in this changed situation, selection of migrants involves a difference in physique between those who migrate and those who do not. As these later migrants come from a population a sample of which had already been measured in Paracho in 1948, this question could be answered simply by finding out which of the individuals in the sample had been hired under the new regime for work in the United States. By means of a census of Paracho taken in September 1952 we determined that of the 297 adult males measured 4 years earlier, 61 had been to the United States subsequent to 1948.

A comparison of their measurements with those who had not gone again since that year shows no important differences (see table 1). Those who went to the United States during the years 1948-1952 had, on the average, significantly broader hands, shallower chests, shorter chins, and shorter ears. The occurrence of only 4 differences as great as twice the standard error is hardly meaningful in an array of 26 measurements. Nevertheless, three of the 4 significant differences correspond to general tendencies which are suggested by the direction of the mean differences in related measurements: 1. The greater hand breadth in migrants is associated with some tendency to greater general size in stature, sitting height, biacromial diameter and all measurements on either extremity. 2. The smaller chest depth in migrants is accompanied by a possible tendency toward narrower chests and toward some smaller breadth and depth dimensions of the face and head and of head height. 3. The smaller ear height is accompanied by a tendency toward smaller ear breadth and narrower nose breadth. The shorter lower face, however, is accompanied by a tendency toward longer face in general.

It was already clear from our previous studies that migrants who, before 1948, had been in the United States during their growing years differ significantly and in characteristic ways from those who had never been or who had first gone when older (Lasker '52). It therefore

TABLE 1

*Differences in Dimensions between 1948-1952  
Migrants and Non-migrants*

	MIGRATED 1948-1952			NOT MIGRATED 1948-1952			UN- WEIGHTED DIFFER- ENCE Mean	DIFFERENCE WEIGHTED FOR PAST MIGRATION Mean	DIFFER- ENCE WEIGHTED FOR AGE Mean
	No.	Mean	± s.e.	No.	Mean	± s.e.			
Stature	61	1638.39	7.69	229	1622.41	3.71	+15.98	+5.19	+10.24
Sitting height	59	861.34	4.00	228	854.61	2.02	+6.73	+3.17	+2.96
Arm length	60	742.05	4.15	233	736.77	2.02	+5.28	+2.22	+3.38
Radius length	60	249.80	1.68	235	248.72	0.80	+1.08	+0.18	+0.54
Hand length	61	181.02	1.13	233	180.86	0.53	+0.16	-0.51	-0.03
Hand breadth	61	81.97	0.54	236	80.55	0.23	+1.42*	+0.97	+1.45*
Tibia length	60	371.97	2.69	234	369.79	1.32	+2.18	+1.28	+1.13
Foot length	60	251.52	1.53	232	249.16	0.70	+2.36	+1.43	+1.67
Biacromial	61	387.46	2.14	233	383.70	1.24	+3.76	+1.29	+2.53
Chest width	61	277.97	2.05	233	279.60	1.31	-1.63	-3.42	+0.88
Chest depth	61	220.95	2.21	235	226.57	1.13	-5.62*	-7.15*	-1.34
Head length	61	188.08	0.82	235	188.45	0.43	-0.37	-0.92	-0.34
Head breadth	61	146.10	0.61	235	147.02	0.36	-0.92	-1.23	-0.69
Head height	61	127.11	0.78	235	128.11	0.34	-1.00	-1.31	-1.20
Minimum frontal	61	104.02	0.48	236	104.12	0.29	-0.10	-0.50	-0.67
Bizygomatic	61	136.84	0.66	235	136.96	0.34	-0.12	-0.54	+0.79
Bigonial	61	103.84	0.78	236	104.76	0.37	-0.92	-1.21	-0.12
Total facial hgt.	61	124.13	0.85	236	123.63	0.43	+0.50	-0.21	+0.31
Upper facial hgt.	60	74.50	0.63	211	74.14	0.31	+0.36	-0.02	+0.10
Lower facial hgt.	60	43.12	0.35	221	44.07	0.23	-0.95*	-1.14*	-0.68
Mouth width	61	56.85	0.54	233	56.68	0.26	+0.17	+0.18	+1.02
Interocular width	61	33.11	0.29	234	32.72	0.18	+0.39	+0.21	+0.58
Nose height	61	55.54	0.40	235	55.39	0.23	+0.15	-0.10	+0.41
Nose breadth	61	40.89	0.43	236	41.04	0.22	-0.15	-0.23	+0.77
Ear length	61	65.92	0.43	236	67.7	0.32	-1.85**	-1.97**	-0.20
Ear breadth	61	35.49	0.33	236	36.02	0.21	-0.53	-0.88*	+0.23

\* Two to three times the standard error of the difference.

\*\* Three or more times the standard error of the difference.

seemed possible that the differences between the migrants and non-migrants of 1948-1952 simply might be due to the fact that disproportionately large numbers of them were drawn from certain groups of previous migrants. Table 2 shows that previous migrational experience was a significant determinant of migration during the period 1948-1952.

TABLE 2

*Male Migrants and Non-Migrants in 1948-1952 according to the Duration of their Previous Migration and to the Age at which they had first gone*

MIGRATION PRIOR TO 1948 <sup>1</sup>	MIGRATION DURING 1948-1952				
	NEGATIVE		POSITIVE		TOTAL
	No.	%	No.	%	No.
I. Never	95	86	16	14	111
II. Before age 17 for 2 or more years	21	70	9	30	30
III. 17-27 for 2 or more years	51	77	15	23	66
IV. 15-27 for 1 year	18	60	12	40	30
V. 27 or over for 1 year	36	82	8	18	44
VI. 27 or over for 2 or more years	14	93	1	7	15

$$\chi^2 = 12.1$$

*p* with 5 degrees of freedom < .05

<sup>1</sup> One individual born in the United States is omitted.

Those who had previously been to the United States when 15 to 27 years old and who had returned to Mexico within 18 months were disproportionately numerous among the 1948-1952 migrants.

For each dimension the difference between the 1948-1952 migrant and non-migrant series was therefore weighted. This was done by taking separately the difference within each class of migrational experience. When these differences are multiplied by the proportion of 1948-1952 migrants in the respective subgroups, the sum is the mean difference weighted for past migration. As an approximate measure of the significance of these weighted differences one can use the standard errors derived from the unweighted means. This will tend to exaggerate the significance of differences, but as the hypothesis is that some of the differences between migrants and non-migrants may be ascribed to previous migrational history, the error will be in the direction of conservatism. As is shown in table 1, the difference in hand breadth between migrants and non-migrants during 1948-1952 is no longer significant.

However, the difference in ear breadth becomes significant. As the subgroups which average generally larger are over-represented among the 1948-1952 migrants, allowance for past migrational experience decreases differences in which the migrants are larger and increases differences in which they are smaller.

The selection for re-migration of returned migrants would be even more striking were it not for the fact that so small a percentage of the previous migrants falls in the age ranges within which labor migration is most frequent. Of 39 previous migrants under age 31 in 1948, 42% migrated again, whereas of 52 sedentes of that age only 27% went. Of 44 previous migrants aged 31-40 in 1948, 30% migrated as compared with only one (3.6%) of 28 sedentes. And of 112 previous migrants over 41 years old in 1948, 14.3% migrated again, whereas only one (3.2%) of 31 sedentes in this age group migrated.

Age is thus also an important factor in selection of migrants. As may be seen in table 3, a higher proportion of the 1948-1952 migrants are drawn from the younger adults measured in 1948.

TABLE 3

*Male Migrants and Non-Migrants during 1948-1952 according to Age in 1948*

AGE	MIGRATION DURING 1948-1952				TOTAL No.
	NEGATIVE		POSITIVE		
	No.	%	No.	%	
18-20	14	70	6	30	20
21-30	38	61	24	39	62
31-40 <sup>1</sup>	58	81	14	19	72
41-50	51	80	13	20	64
51-up	74	95	4	5	78

$$\chi^2 = 25.0$$

$p$  with 4 degrees of freedom  $< 0.0001$

<sup>1</sup> One individual born in the United States is omitted.

Many of the measurements under study are known to vary with age (Lasker, '53). If allowance is made for the changes in dimension with age, what can one say of differences between those who went to the United States after 1948 and those who did not? Age differences have been weighted in a manner exactly analogous to the way in which past migration was taken into account.



As may be seen in table 1, the age factor accounts for the significant differences in chest depth, lower facial height and ear height. Only the hand breadth difference remains unaccounted for by the change in age composition. Those who have unsuccessfully applied for contracts state that the agents of the United States Department of Agriculture, by whom they were interviewed concerning labor-contracts, inspect their hands. This was done, they say, to exclude those who seemed unaccustomed to hard manual work. One local story tells of a shopkeeper who dipped his hands in lime to harden them like a farmer's; the "Gringo," apparently detecting the ruse, told him that his hands were too rough and that he should go home and take a rest. Another anecdote tells of a barkeeper who was repeatedly refused a permit until he was accepted one day after he had cut and scratched his hands in a fall while drunk. It is interesting, therefore, that greater hand breadth—which might be selected for during these examinations—is the one measurement which is significantly larger in migrants even after allowance is made for age. But, as noted above, the difference in hand breadth is not significant when allowance is made for past migration. Furthermore, one might well expect at least one measurement to show this extent of difference just by chance.

In conclusion, there is little evidence of physical selection of migrants from Paracho to the United States even during a period when only a small proportion of those who want to work there are given labor contracts. When the total series is considered, or when allowance is made for the undoubted selection of those who have migrated before, a few minor differences may be statistically significant. But when the age distribution of those selected is taken into account, the mean differences in measured dimensions between this group of migrants and non-migrants are adequately explained. There is selection for age and past migration, and probably for knowledge of English, past occupation, and industrial skills. There is also an economic selection at least to the extent of means to reach the community where the contracts are made, and frequently to pay bribes to get an interview with the proper authorities. With adequate means to do so, a few men who had been rejected were able to go to the United States on their own (either legally or as "wetbacks"). These factors so override in importance whatever considerations of physique might otherwise influence the choice of workers by the United States agents that—with possibly the single exception of hand breadth—no evidence of physical selection was found.

This conclusion is derived, however, from data concerning a single small community—a community peculiar in that migration to the United States is a common expectation of young men. It remains a question to what extent the widely held notion of physical selection of migrants may hold for other groups, but among at least some groups of labor migrants, such selection is evidently insignificant.

### LITERATURE CITED

- LASKER, G. W. 1952 Environmental growth factors and selective migration. *Human Biol.*, 24: 262-289.
- 1953 The age factor in bodily measurements of adult male and female Mexicans. *Human Biol.*, 25: 50-63.





# FAT PATTERNING AND FAT INTERCORRELATIONS IN THE ADULT MALE

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## INTRODUCTION

THE investigation of subcutaneous fat has at least two somewhat divergent objectives. The first objective is descriptive: to establish the patterning and changes in subcutaneous fat, differences in thickness throughout the body from infancy through advancing age. The second objective is to determine the interrelationship among the different fat thicknesses measured, and the relationship between subcutaneous fat and the total body fat.

Information on subcutaneous fat thickness is most abundant for children, where fat-caliper measurements have been supplemented by teleoroentgenography since 1939. Data on fat thickness intercorrelations in childhood are also available for three age levels (Reynolds '51). Information on adults, however, is more limited. With the exception of leg fat (Reynolds and Grote '48, Reynolds '48, '51, and Garn and Saalberg '52) contemporary adult data is almost entirely based on skin-fold measurements. Since the skin-fold technique is difficult to execute on certain areas of the body, and the x-ray method affords a more precise localization of fat-thickness measurements, further data on patterning and intercorrelations are to be desired especially on adults.

It is the purpose of this paper to provide data on the patterning of subcutaneous fat in the adult male, and to explore the intercorrelations among the different regions. It is the further purpose of this paper to discover which sections of the *tela adiposa* are more indicative of body fat in general, and to determine the relationship between fat thickness and weight.

## METHODS AND MATERIALS

The present study is based on soft-tissue teleoroentgenograms of 87 healthy white males, ranging from 20-69 years of age. With one

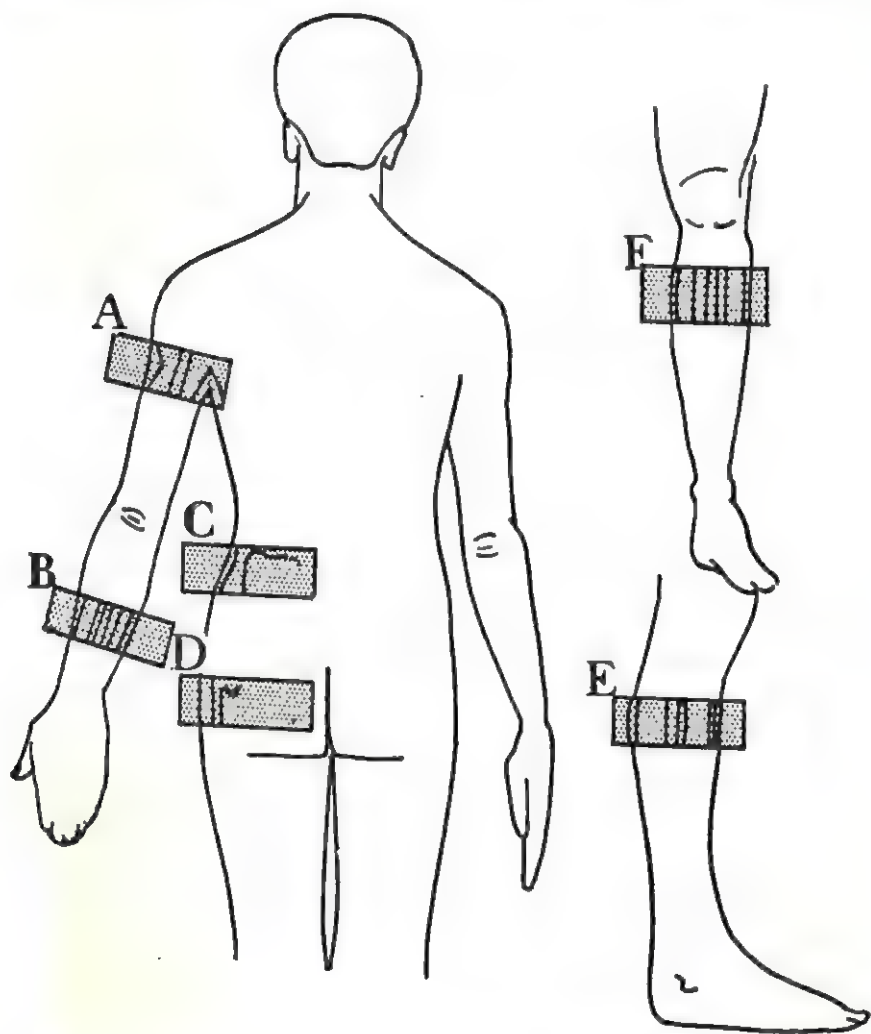


FIG. 1. Location of X-ray "sections" described in the text: A. deltoid insertion section; B. lower arm section; C. iliac section; D. trochanteric section; E. antero-posterior leg section (lateral view); F. transverse leg section (A-P view).

exception all were regular participants in the Fels study, being for the most part parents of children enrolled in the longitudinal program.



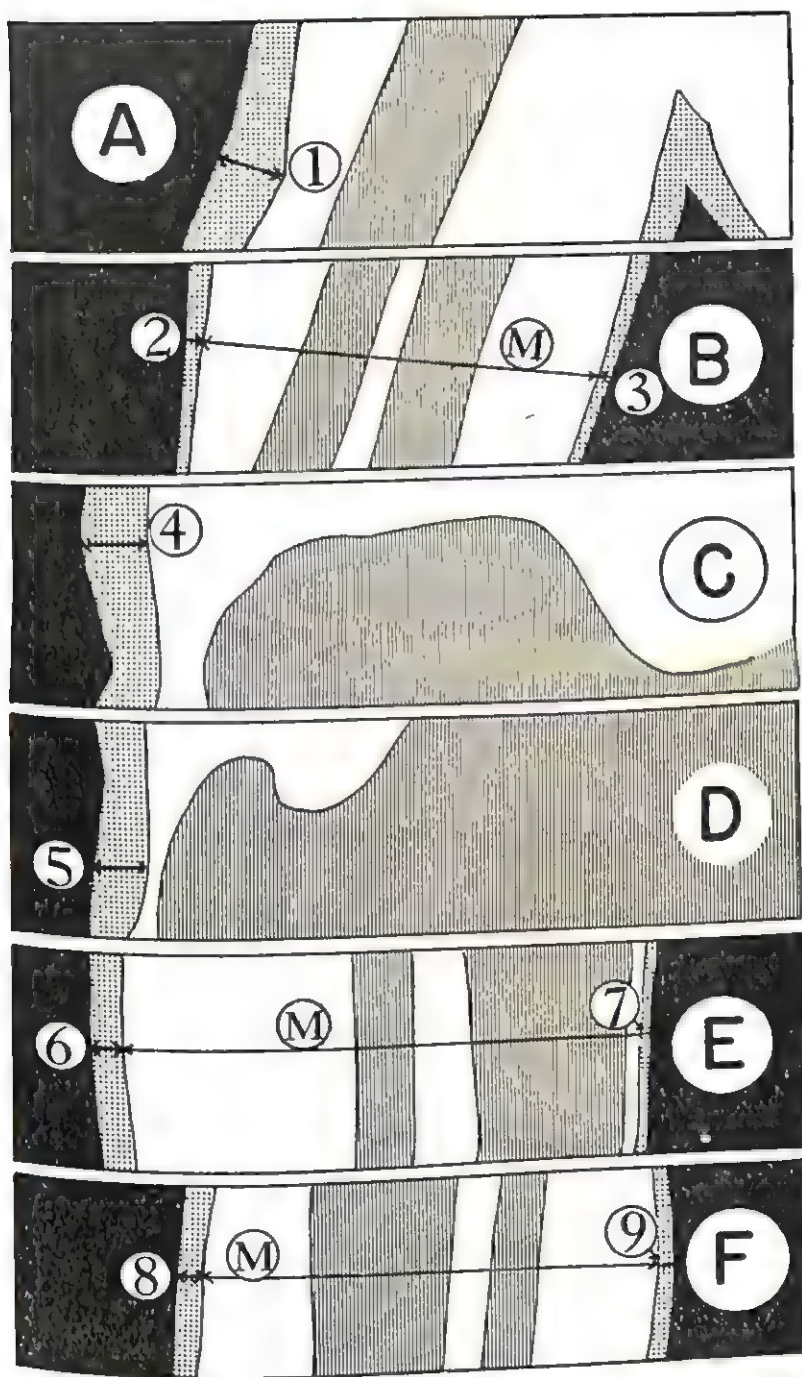


FIG. 2. Tracing of an X-ray series showing fat thicknesses measured in this study: M. level of maximum muscle diameter; 1. deltoid insertion; 2. lateral arm; 3. medial arm; 4. iliac; 5. trochanteric; 6. posterior leg; 7. anterior leg; 8. medial leg; 9. lateral leg. Sections lettered as in Fig. 1.

All were native born, and most were lifelong residents of southwestern Ohio. One active but extremely obese man, weighing 307 pounds, is not represented in the means, but is included in the intercorrelations.

The x-rays were taken at a standardized 6 foot tube-to-film distance, at 14 milliamperes seconds, with peak kilovoltages appropriate to the part thickness. A total of 6 x-ray "sections" were taken of each subject, as follows: A. deltoid insertion section; B. lower arm section; C. iliac section; D. trochanteric section; E. lateral calf view, and F. antero-posterior calf view. The location of these sections, as well as the standard poses used are shown in figure 1.

Fat thicknesses, or more precisely the thickness of the skin plus the fat-containing tissue were measured directly on the x-rays, using a vernier caliper with ground tips (Garn and Saalberg '53); measurements were made at right angles to the skin surface. The nine fat measurements included: 1. deltoid insertion fat; 2. medial arm fat; 3. lateral arm fat; 4. iliac fat; 5. trochanteric fat; 6. posterior leg fat; 7. anterior leg fat; 8. medial leg fat; and 9. lateral leg fat. Thicknesses 1, 4 and 5 were taken in reference to fixed anatomical points. Thicknesses 2 and 3, and 6 and 9 were taken at mid-arm and at the level of the maximum muscle diameter respectively. These measured thicknesses and their location are shown in figure 2, which is a tracing of an actual set of x-rays.

Two sources of error may be mentioned, magnification (angular distortion) and tissue hydration. Since the focal film distance was constant, magnification is reasonably consistent within each body area considered. The systematic errors, therefore, do not appreciably affect the mean values and do not affect the intercorrelations. Errors due to tissue hydration were minimized both by confining the data collection to a three month period (May to early July, 1953), and through the use of air conditioning.

#### FINDINGS

As shown in table 1, the 87 men in this study averaged 176.6 cm in stature, 76.4 kg in weight and 40.8 years in age. In height and weight they come close to reported values for men of comparable age and economic status (Brožek and Keys '51, Brožek '52).

The thickness of the subcutaneous fat deposits measured here, varied from an average of 18.9 mm over the iliac crest to 2.7 mm (including skin) over the tibia. The thickest fat layers measured were located over the pelvis and at the deltoid insertion, the thinnest on the medial

aspect of the forearm, and on the anterior leg. Ranked in descending order of thickness, the fat sequence was iliac, deltoid, trochanteric, posterior leg, medial leg, lateral leg, lateral arm, medial arm, and anterior leg. Iliac fat, in addition to being thickest, also showed the greatest absolute variability.

While the ranking given above, based on the mean thicknesses, provides an idea of the relative fat thickness at the 9 sites measured, it was not the modal sequence. In some individuals deltoid fat was the thickest, in others iliac fat. Fat rankings were closely related to the total amount of fat, and to total body weight. Thus, in individuals weighing under 74 kg, deltoid fat exceeded other thicknesses, while at 75 kg and above, iliac fat was the thickest (table 1). This shift in thickness rankings was also evident in comparing younger and lighter subjects to older and heavier subjects.

TABLE 1  
*Body Size, Fat Thicknesses, and Fat Rankings*

MEASUREMENT	NO.	MEAN	S. D.	C. V.	FAT RANKING	RANKING	
						LIGHTER MEN <sup>1</sup>	HEAVIER MEN <sup>2</sup>
Age (yrs)	87	40.8	11.1	27.2			
Height (cm)	86	176.6 ± 0.5	4.9	2.8			
Weight (kg)	87	76.4 ± 1.0	9.1	11.9			
Deltoid fat (mm)	86	17.8 ± 0.5	4.5	25.3	2	1	2
Lateral arm fat	86	4.6 ± 0.2	1.7	36.9	7	7	7
Medial arm fat	86	3.5 ± 0.1	1.3	37.1	8	8	8
Iliac fat	83	18.9 ± 0.9	8.3	43.9	1	2	1
Trochanteric fat	82	16.6 ± 0.8	6.9	41.5	3	3	3
Posterior leg fat	84	7.2 ± 0.3	2.5	34.7	4	4	4
Anterior leg fat	81	2.7 ± 0.1	0.7	25.9	9	9	9
Medial leg fat	84	6.3 ± 0.3	2.4	38.1	5	5	5
Lateral leg fat	84	4.7 ± 0.2	1.6	34.8	6	6	6

1. Men weighing between 50 and 74 kg.
2. Men weighing between 75 and 100 kg.

All of the 9 fat thicknesses were positively and significantly inter-correlated, with values of  $r$  ranging from 0.33 to 0.79 as shown in table 2. The regression lines were prevailingly linear, thus indicating that  $r$  rather than  $\eta$  was the appropriate measure of covariance. How-

TABLE 2  
*Intercorrelations among Fat Layers*

MEASUREMENT	1. DELTOID	2. LATERAL ARM	3. MEDIAL ARM	4. ILIAC	5. TROCANTER	6. POSTERIOR LEG	7. ANTERIOR LEG	8. MEDIAL LEG	9. LATERAL LEG	10. WEIGHT
1. Deltoid Insertion	—	.67	.54	.74	.75	.44	.50	.02	.56	.67
2. Lateral Arm	.67	—	.68	.62	.68	.37	.56	.59	.50	.62
3. Medial Arm	.54	.68	—	.48	.65	.38	.52	.70	.40	.21
4. Iliac	.74	.62	.48	—	.75	.33	.46	.50	.44	.63
5. Trochanter	.75	.68	.65	.75	—	.44	.68	.79	.61	.71
6. Posterior Leg	.44	.37	.38	.33	.44	—	.43	.56	.53	.41
7. Anterior Leg	.50	.56	.52	.46	.68	.43	—	.79	.62	.61
8. Medial Leg	.62	.59	.70	.50	.79	.56	.79	—	.51	.71
9. Lateral Leg	.56	.50	.40	.44	.61	.53	.62	.51	—	.29
10. Weight	.67	.62	.21	.63	.71	.41	.61	.71	.29	—



ever, as shown in table 2, trochanteric fat, medial leg fat, and deltoid fat generally exhibited higher intercorrelations with the various fat thicknesses, than did lateral arm fat, lateral leg fat and especially posterior leg fat.

In order to obtain a more acceptable index of the relationship between any one fat measurement and the remaining 8, than could be obtained from the mean  $r$ , the values in table 2 were transformed into  $z$  values (the  $z$  transform of  $r$ ), using table V-B in Fisher ('48). The  $z$  values, for each thickness, were then averaged, as shown in table 3.

TABLE 3

*Rankings of Predictive Efficiency and Relative Variability for 9 Fat Thicknesses*

FAT THICKNESS	MEAN $Z^1$	$Z$ RANKING	C. V. <sup>2</sup>	VARIABILITY RANKING
1. Deltoid Insertion	.60	3	25.3	9
2. Lateral Arm	.54	7	36.9	5
3. Medial Arm	.58	4	37.1	4
4. Iliac	.54	6	43.9	1
5. Trochanteric	.67	1	41.5	2
6. Posterior Leg	.44	9	34.7	7
7. Anterior Leg	.57	5	25.9	8
8. Medial Leg	.63	2	38.1	3
9. Lateral Leg	.52	8	34.8	6

<sup>1</sup> From data in table 2 and table V-B in Fisher ('48).

<sup>2</sup> From table 1.

It is evident, in this table, that trochanteric fat and medial leg fat are more highly covariant with the other layers, while lateral and posterior leg fat have less in common with the other fat measurements.

The question arose as to whether the predictive efficiency of a fat layer is related to its average thickness. Accordingly thickness rankings (from table 2) were correlated with mean  $z$  rankings (from table 3) using Spearman's  $\rho$  formula (Edwards '49). The obtained  $\rho$  of 0.22 could not be considered significantly different from zero. It is not likely, therefore, that thickness, per se, is indicative of the degree of communality exhibited by a given fat deposit. Nor does the location of the fat enter, as is evident in table 3. The three "best" predictors of fat thickness in general are widely separated in anatomical space, while the second best and the poorest are but centimeters apart.

Finally, an attempt to discover a relationship between predictive efficiency and relative variability of the different fat measurements was no more successful, the obtained  $\rho$  being 0.23.

It is of interest to note that trochanteric and medial leg fat exhibit the highest correlations with gross weight ( $r = 0.71$ ) while the remaining fat measurement lag behind, just as they did in the mean  $z$  values. These correlations serve to show that fat, while not the only determinant of weight, accounts for much of the interpersonal variance, up to 50% in the age group considered, and they suggest that the fat weight, as distinguished from the total body weight, may be estimated from trochanteric or medial leg fat measurements using the ordinary regression equations.

#### DISCUSSION

It is evident, from the findings reported here, that the thickness of the *tela adiposa* varies both between anatomical regions, and within such regions. In the adult male, the fat deposits over the pelvic region are the broadest, averaging 4 times as thick as the fat on the lower arm, and 6 times the thickness of the fat over the tibia. But on the lower leg (to take just one anatomical region) the fat layer is far from uniform. Medial leg fat is consistently thicker than lateral leg fat, and the fat on the back of the leg averages more than twice as thick as the fat on the front. And, as the total amount of fat increases, there is an alteration in the relative thickness of some of the fat layers. Thus in leaner males, deltoid insertion fat is the thickest single deposit, while in males over 75 kg in weight, iliac fat exceeds all other thicknesses.

As might be expected, all 9 fat thicknesses measured here are positively and significantly intercorrelated, with values of  $r$  ranging from 0.33 to 0.79. However, some of the fatty deposits exhibit a higher general covariance than others. Trochanteric fat shows both the highest correlation with weight (0.71) and the highest mean  $z$  (0.67); medial leg fat and deltoid fat also tend to vary directly with the other fat thicknesses, and to be moderately correlated with gross weight. Posterior leg fat exhibits the least tendency toward group covariance. Evidently absolute fat thickness is no indication of the predictive efficiency of a given fat measurement, nor in fact is location. Medial leg fat, though a notably good index of general fat thickness, is far from being the thickest deposit, and is situated in proximity to the poorest predictors of fat in general. At present, therefore, no general rule for predetermining the most representative fat deposit can be formulated.

Comparing the intercorrelations obtained here, with others given in the literature, the values appear to be reasonably similar. Of the three age groups investigated by Reynolds ('51) the intercorrelations obtained on these 87 adult males are comparable to his 7 and 11 year olds, but are lower than those for his 15 year old boys. While Brožek and Keys ('51) measured different fat thicknesses and used a different technique (skin-folds) it is interesting to see that their intercorrelations were of the same magnitude for males of comparable age, but markedly higher for younger males (mean age 21). There is a suggestion, therefore, that subcutaneous fat varies as a unit near the time of peak androgen production, while at other ages local autonomies exert a greater influence.

From the standpoint of nutritional anthropometry, it would seem that the simple bitrochanteric diameter, taken as a "contact" measurement might satisfactorily meter fluctuations in body fat. Trochanteric fat, it is seen, correlates well with gross weight, it intercorrelates well with other fat thicknesses, and the total range of thickness is large. At the same time since the traditional bi-iliac measurement includes an average of 4 cm of fat in this age group, one would hesitate to accept it as an approximation to the true skeletal dimension.

If a single fat measurement, as determined from soft-tissue x-rays, is desired for nutritional or physiological research, preference would obviously be extended to trochanteric fat or to medial leg fat. Both are representative of fat in general, and both vary directly with weight. Technically, the antero-posterior leg view is the simpler, and the least inconvenient to the subject. Brožek, it may be recalled, doubted the use of the calf section, writing that "biologically it seems to be a questionable indicator of the general level of fat content" (Brožek '53, p. 157). While this is true of posterior leg fat, it is by no means true of medial leg fat. In all likelihood Brožek made this pessimistic prediction in the absence of data on fat intercorrelations.

While the present study stresses the way the subcutaneous fat layer behaves as a unit, despite regional differences in absolute thickness, this is but part of the total picture. The *tela adiposa* is a single sheet, its volume is related to the volume of the inner fat, and it is possible to estimate the fat weight or percentage of fat of an individual from a given measured thickness. At the same time there are marked inter-personal differences not just in the amount of fat, but in the way fat is distributed. One man may be fat, but with less fat on his legs than would be predicted from his absolute fat content. Another may have

little fat, but with more on his legs than might be expected. The extent of such individual deviations from their own baseline (or mean  $z$  score) is a problem in its own right, and one that cannot be approached through the calculations of the weight of fat, or the percentage fat. Hence the need for regional fat measurements, as well as measurements or estimates of the total body fat.

#### SUMMARY

1. Patterning and intercorrelations in subcutaneous fat thickness were investigated, through the use of teleoroentgenograms, on 87 active white males aged 20-69 years.

2. Mean fat thickness ranged from 18.9 mm (iliac fat) to 2.7 mm (anterior leg fat). Mean thickness rankings were (in decreasing order) iliac fat, deltoid fat, trochanteric fat, posterior leg fat, medial leg fat, lateral arm fat, lateral leg fat, medial arm fat and anterior leg fat.

3. Absolute thickness rankings changed with increasing weight, thus deltoid-iliac-trochanteric was characteristic of leaner men, and iliac-deltoid-trochanteric was more common among fatter men.

4. Intercorrelations among the 9 fat thickness ranged from 0.33 to 0.79.

5. Trochanteric and medial leg fat showed the highest intercorrelations, and correlated well with gross weight, while lateral and posterior leg fat exhibited a greater degree of autonomy.

6. Neither mean thickness nor anatomical location provided a guide to the predictive efficiency of a fat layer.

7. Attention was drawn to the distinction between studies relating to the total fat volume and those concerned with individual differences in the patterns of fat deposition.

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## LITERATURE CITED

- BROŽEK, J. 1952 Changes of body composition in man during maturity and their nutritional implications. *Fed. Proc.* 11: 784-793.
- 1953 Measuring nutriture. *Am. J. Phys. Anthropol. N. S.* 11: 147-180.
- BROŽEK, J., AND A. KEYS 1951 The evaluation of leanness-fatness in man: norms and interrelationships. *Brit. J. Nutrit.*, 5: 194-206.
- EDWARDS, A. L. 1947 Statistical analysis. Rinehart and Co. New York.
- FISHER, R. A. 1948 Statistical methods for research workers. 10th rev. ed., Oliver and Boyd, Edinburgh.
- GARN, S. M., AND J. H. SAALBERG 1953 Sex and age differences in the composition of the adult leg. *Human Biol.*, 25: 144-153.
- REYNOLDS, E. L. 1948 Distribution of tissue components in the female leg from birth to maturity. *Anat. Rec.* 100: 621-630.
- 1951 The distribution of subcutaneous fat in childhood and adolescence. Monographs of the Society for Research in Child Development. 15(2) Serial No. 50, for 1950.
- REYNOLDS, E. L., AND P. GROTE 1948 Sex differences in the distribution of tissue components in the human leg from birth to maturity. *Anat. Rec.* 102: 45-54.



## BOOKS RECEIVED

- SCIENCE AND MAN'S BEHAVIOR. By Trigant Burrow. xii + 564 pp. Philosophical Library, New York, 1953. \$6.00.
- THE ADAPTIVE CHIN. By E. Lloyd DuBrul and Harry Sicher. ix + 97 pp. Charles C. Thomas, Springfield, Ill., 1954.
- CURIOUS CREATURES. By Erna Pinner. 256 pp. Philosophical Library, New York, 1953. \$4.75.



# HUMAN BIOLOGY

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## CULTURAL FACTORS AFFECTING THE STUDY OF HUMAN BIOLOGY

THE existence of a field called human biology and the need for a distinct journal bearing this name, may be justified in one of two ways. Attention may be drawn to the unique taxonomic position of man. Alternatively, attention may be directed to the behavior of man, which differs markedly from group to group. The first justification rests on biological grounds. The second justification takes cognizance of the existence of culture.

As to man's unique position in nature, the magnitude of the biological differences now seems less and less. The bipedal gait, and the upright posture, no longer can be claimed as exclusively human. Relative hairlessness turns out to be a characteristic shared by other anthropoids, and in this respect they may occasionally surpass man. In motor development the young chimpanzee is more than superficially like the human infant. And it turns out that other anthropoids can use symbols, invent tools, and solve abstract problems. Anatomically, biochemically, and physiologically, it becomes increasingly difficult to demonstrate in what respects man is completely unique. Yet it is still true that we can not investigate human biology in quite the same fashion that we

investigate the biology of some other species, because of the cultural factor.

For most species, we can assume randomness of mating. True, animals do have preferences (in this respect too they are "human") and the sexual stimulus value of females exhibits a wide range of variation. But such preferences are not systematized within a breeding population. Animals do not seek prior information about prospective mating partners, nor do they eschew potential spouses because of consanguinity, voluntary affiliations, or political or religious beliefs. In man, however, the existence of traditions directing the choice of mates, or limiting the choice to a particular individual out of many, is so common that truly random mating may be considered unlikely for all but the smallest and least complex groups. Or, to put it differently, in what other animal does a railroad track serve as an effective barrier to gene flow? In what other species may the mating pattern involve marriage to two sisters, or a woman and her daughter?

For most animal forms it is possible to observe the dietary range and therefore to make certain inferences as to their metabolic requirements. In some cases, an extremely limited dietary range gives immediate indication of a metabolic peculiarity. But in man, any attempt to estimate the dietary range from the food habits of a particular group runs into early failure. For food prohibitions, learned eating preferences, and culturally-defined limits on what is considered edible, limit the individual to a fraction of what is actually palatable, reasonably nutritious, and satisfying. Not infrequently it is found that a weed (a plant considered inedible) is a superior source of nutrients, while a time-honored cultivated plant proves hardly worth the boiling.

Similar problems arise in studying fecundity, fertility, or their prelude sexual activity. For here biology is thoroughly submerged by cultural practices. The birth rate, crude or corrected, is at best only a partial indication of the reproductive potential. It is affected by the mean age of marriage, the extent of sexual activity (including ritual taboos) and what the members of the group choose to do about conception. And, in discussing sexual activity, the extent of cultural influences can hardly be overestimated. There are marked differences in what is considered to be a "normal" coital frequency. Moreover, sexual behavior may be altered by changes within the culture, or even by disseminating statistical information about sexual behavior! To find a parallel in any other species would be difficult indeed.



While the problem of obtaining culture-free biological data on human beings is difficult enough, the problem of applying data (known to be culture-influenced) for human betterment, is especially hazardous. In our desire to improve the nutritional status of other peoples, we attempt to instill our own dietary practices. Yet there is little evidence at present that three meals a day, as contrasted with two or one, is a physiological necessity rather than just a particular way of our own.

And there are times when physiological data seem strongly culture bound. To an American, British insistence that the custom of mid-afternoon tea is the natural result of the afternoon fall in blood sugar sounds like a rationalization. It is legitimate to enquire whether comparable changes in blood sugar also occur in subjects not habituated to the taking of tea, and whether the pattern demonstrated in Britain may not be an anticipatory response rather than a portent of impending hypoglycemia.

These various examples serve to demonstrate the extent to which cultural practices intrude into the study of human biology, making it quite different from the study of any other species. They also indicate the kind of information that the human biologist needs to have, above and beyond the information ordinarily required in biological research.

#### CULTURAL FACTORS AND PROBLEMS IN HUMAN GENETICS

The extent to which cultural factors have to be reckoned with is extremely apparent in human genetics, especially population genetics, as compared to family-line or pedigree analyses. In shifting from rare, usually pathological traits, to common and non-pathological characteristics, the easily defined lineage has been replaced by the more nebulous "population." And this latter unit is by no means identical with the horde or tribe on the one hand, or the city or state on the other.

Suppose that we are interested in the population frequencies for  $p$ ,  $q$  and  $r$  and are given a small group and have reasonable evidence that the group is endogamous, not divided into moieties, and not overly weighted by a single lineage, the observed frequencies for the group are in fact population frequencies. (We assume that the total group is represented, or alternatively that the serologist avoided typing his informant's lineage exclusively.) But how about a larger group, made up of two, four or more distinct breeding populations? Firstly, does the serologist know of the existence of these sympatric yet reproductively

isolated populations? Secondly, how does he go about identifying the breeding group to which each subject belongs?

Further examples of the same situation exist in every large city, wherein a dozen or more breeding groups are partially concealed by uniformities of language and dress. Cities are economic units to be sure; they are also political units and demographic units. But, as in Boston or Vienna, cities are not populations in the genetical sense. The distinct breeding groups may be markedly different in gene frequencies. In extreme cases, as in Indian cities, divisions of a single hereditary occupational class (caste) may differ as much as Negro and White in Baton Rouge, Louisiana. Under these circumstances data on the blood groups of New York City, or the blood groups of Rochester, New York, need not provide information on "population" genetics, useful though they are in many other ways.

For obvious reasons, hospital patients have been a favorite source of genetical information. They are at least temporarily incarcerated, they expect to be questioned and bled, and (assuming that disease is no respecter of persons) they should be relatively unselected. But hospital patients are not random representatives despite the anonymity provided by a hospital gown.

Out-patients, and to a lesser extent, ward patients come from the hospital's immediate vicinity and thus reflect the composition of the adjacent districts. If the district is Irish, so will be the out-patients, even though the hospital bears a Hebrew name. In Boston the Massachusetts General Hospital, located in a region of cold-water flats, includes a disproportionate number of Italian patients, though the more exclusive Phillips House attracts the expensively sick from all the world. The Peter Bent Brigham, on the other hand, draws more heavily from the Jewish quarters of Brookline and Roxbury. Such differences in out-patient origin may also be observed in the hospitals of New York City or London. Under these circumstances, estimates of gene frequencies based on out-patients alone may have a limited value, while attempts to show race-associated disease predisposition may be prejudiced by the simple matter of just where in a city a hospital is located.

The fact that immigrants settle in the least expensive section of a city, close to fellow nationals, is a boon to the human geneticist. Locating one Maloof in the phone book locates an entire Syrian community, just as locating one Slovene provides the entré to many. Because migrations often take place on a family-wide, community-wide, or city-wide basis.

it is possible to sample the genetic composition of an Albanian village in Boston, or an Armenian province in Providence; to locate Iroquois Indians, contact structural-steel workers in Rochester!

But the very facts that migrations do take place on a family-line basis (not as isolated individuals of either sex) and religious conversions are not distributed at random, make more difficult such tasks as the demonstration of "genetic drift" in man. Were migration an individual matter, or the joining of religious isolates restricted only to sexually mature but unmarried males and females, demonstrating drift would be reasonably simple. All that would be necessary would be the comparison of gene frequencies in the migrant group or in the descendants of the original converts, with gene frequencies in the parental population (or their descendants). But the simple facts that people do not migrate at random, unrelated men and women of breeding age are not suddenly cut off from their tribe, and randomly sampled men and women do not run off and join a religious community, provide a serious problem for those interested in demonstrating drift. For the migrants most likely included families, the adults, cut off by flood or earthquake probably were related, while the sect leaders probably converted entire families, and related families at that. Under these circumstances it is legitimate to ask whether the prerequisites for the successful demonstration of genetic drift in man will ever be met.

It is evident, then, that the study of human genetics is thoroughly complicated by the existence of culture. Statistical corrections have to be made for polygamy, polygyny, and cross-cousin marriage, to say nothing of the sororate, the levirate and marrying one's deceased wife's mother. Because the population unit-of-study is not identical with the township, city or community, the geneticist must have prior information on what breeding groups actually exist. In dealing with hospital patients, the notion has to be suppressed that in their nightgowns they are a random sample of anything. And the systematics of human behavior practically provide a guarantee against the possibility that any group united by binding ties will be composed of "randomly" selected men and women. Therefore conditions suitable for the demonstration of drift may be extremely difficult to document in man.

## CULTURAL FACTORS AND THE STUDY OF HUMAN GROWTH

In contrast to human genetics, where the complexities of mating systems only recently have begun to attract interest, research in human growth has been characterized by a formal appreciation of cultural differences. In fact many studies have been specifically designed to show the extent of cultural influences. The growth of children of similar stock, but under different cultural conditions, has been compared. The sizes of children in different cities have been contrasted. Rural-urban differences have been investigated and social class has been given more attention in growth studies than in any other area of human biology.

But if students of growth have been aware of cultural differences in the abstract, they have failed to be specific. Logically, and perhaps correctly, group divergences in body size or in the rate of growth (apart from those differences manifestly racial in nature) have been attributed to dietary differences. Unfortunately, dietary studies have rarely accompanied the measuring of stature, and the taking of weight, so that the prime variable remains unstudied.

Further, the existence of specific cultural practices bearing upon the growth rate has been given little attention. The possibility that child growth is less rapid where voluntary activity is greater has not been considered. Nor has the mean temperature of the home been given attention, despite the close relationship between temperature and involuntary activity.

The middle class American child, reared by moderately authoritarian and relatively apprehensive parents (by global standards), is protected from over-exertion. His play periods are timed, naps are enforced, and care is taken to assure uninterrupted slumber. Children of the lower classes, on the other hand, are treated in more permissive fashion, with less emphasis on rest and a more lenient attitude toward bed-time. Therefore, though the caloric intake may be comparable in the two groups, the caloric expenditure is not. And the difference, caloric intake minus caloric expenditure, represents the energy reserve available for tissue maintenance and growth.

In some cultures even less attention is paid to rest. An African settlement or a Balinese village may operate on a 24-hour schedule with events of interest all the while. There, uninterrupted sleep may be a rarity for the children, with cat-naps alternating with participation



in the village night-life. Such practices further increase the energy expenditure, leaving a minimal reserve for the process of growth.

Besides, the temperature of the home may play an important role. Energy metabolism and temperature are inversely related. As the temperature falls, considerable energy is utilized in maintaining body temperature and in insensible shivering. Under these circumstances the high October-through-April temperatures of the American household (which distress visiting Europeans so markedly) may have a hot-house effect on the children allowing the maximum usage of the energy intake for growth.

In addition to these systematic differences in child-rearing practices, which may bear upon energy metabolism, we should note those practices affecting one sex alone. In many parts of the world, women eat apart from the men, girls get the soup while boys get the meat. Or both sexes may eat with the women until puberty, with the boys transferring to the men's table thereafter. Boy babies may be suckled longer (to make them strong), or weaned earlier (to make them independent). Such child-rearing practices may be expected to have a marked effect upon stature and weight, producing growth curves markedly different from those customarily encountered.

It is not sufficient, then, to be aware of cultural differences in the abstract: rather it is necessary to know enough of the cultural practices to relate them to the growth phenomena under investigation.

#### CULTURE AND HUMAN PERFORMANCE

We have left until last the extremes of human performance and the physiologic concomitants of race. To what extent do cultural practices influence cold-tolerance, heat-tolerance, and load carrying? To what extent have we evidence that races differ in performance levels with the cultural variable ruled out?

In view of the variations in cultural conditioning, it is not unlikely that properly selected "natives" would upset the best laboratory data we have. Malayan pearl divers routinely exceed our breath-holding records. Andean miners mock our need for pressurized planes. The Ona of South America exist in an unclothed state under conditions that would hospitalize Americans for "exposure." Merchants in Mecca, and donkey drivers too, keep busy at a temperature designed to melt myelin. And Korean porters tote ammunition boxes amazingly heavy in respect

to their body weight. While it is not culture itself but extensive physical conditioning that makes such feats possible, it is in particular cultural contexts that they are deemed attainable. As a member of a culture, each individual gains a knowledge of what the extremes of performance are supposed to be and we may presume that under test conditions he reports the limits of his endurance accordingly.

As to racial differences, numerical data are scanty, though hearsay reports are numerous. Eskimo are supposed to have more resistance to cold, an expectable consequence of over 40 centuries of cold selection. Negroes are supposed to exhibit higher heat tolerance, again a not unexpected finding in view of their adaptive zone.

But the available data are far from being culture-free. The most recent tests contrasted Point Barrow Eskimo with whites recently arrived in the arctic. In proving Negro superiority under hot and humid conditions, northern white college students were pitted against southern Negro sharecroppers. It still remains to be seen how real the differences are with the variables of culture removed.

Under these circumstances it would seem that the range of human capacities, including cold-tolerance, heat-tolerance, and load-carrying will have to be reinvestigated with more adequate attention to the cultural factor. As with studies involving nutrition, genetics, or human growth, these more coldly physiological aspects of human biology can not be investigated as if the subjects lived in a cultural vacuum, up to the time they were enlisted as "volunteers" for research.

It is the purpose of this article to show how cultural factors intrude into the study of human biology. Man can not be treated just as a large primate, amenable to the methods and techniques of mammalian biology. The investigation of human biology demands precautions, research methods, and fore-knowledge unparalleled for any other species. And many of the problems in human biology are themselves unique, holding for one human group and not for another.

For some studies, a knowledge of social structure and mating systems may be a prime necessity. For others, detailed information on the dietary habits and techniques of food preparation may be equally important. Still other studies may demand information on contraceptive techniques and local beliefs concerning reproduction. Yet others may hinge on knowing at what age infants are allowed to roam or what restrictions are imposed on pregnant women. Such knowledge is not ordinarily a part of biological research, nor is it needed for a genetically constant

organism, on a standardized diet, reared under laboratory conditions. But for man, with culture a principal variable, information of this sort is an indispensable prerequisite in research.

The existence of the field of human biology, and the need for a journal bearing this name, derive ample justification from the simple fact that the organism in question, man, possesses the quality we call culture.

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## PATTERNS OF GROWTH OF THE SKULL AS REVEALED BY VITAL STAINING \*

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### INTRODUCTION

THE purpose of the study here reported was to determine the processes of bone growth influencing the form of the skull of the rat in order to better understand these processes in mammals in general and in man in particular. The experimental technique of staining the growing bone with alizarin red S was used (1) to reveal the specific sites and modes of growth resulting in an increase in the size of the skull, and (2) to assess the effects of differential growth at these sites in modifying cranial form. The determination of the anatomical factors governing the relationships of the cranial vault, the cranial base, and the face is believed to have implication for the interpretation of morphological differences among related species and for the analysis of changing form and proportion during the ontogenetic development of the mammalian skull.

The nature of the biological mechanisms affecting changes in cranial form is of particular significance for physical anthropology, which is concerned with the analysis of the phylogenetic development of the human skull. Investigators using the techniques of comparative anatomy and anthropometry have described an evolutionary trend among fossil and modern human forms resulting in a general increase in the size of the brain case and reduction in the size of the face and the cranial

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architecture (supraorbital ridges, temporal lines, and nuchal crests). It has generally been conceded that the differences in form and proportion found among fossil and living groups are due to changes in relative rates of growth, but the actual processes have remained obscure, and the differences have been explained largely by inferences drawn from the descriptive data. For example, Weidenreich ('41, '45), on the basis of comparisons of different species of dogs, apes, and men, contends that "the cerebral predominance that characterizes the skulls of dwarf forms and man not only determines the special shape of the brain case proper, but also the size and arrangement of the facial parts and, in connection therewith, the development of the superstructures of the cranium" ('41, p. 378). According to this interpretation, then, the skull is a single system of growth in which the size of the brain alone determines cranial form.

It is significant that Weidenreich uses data drawn from pathology, such as the cranial form of microcephalic skulls, to support his interpretation. De Beer ('37, p. 485) also refers to microcephaly in his explanation of the development of the skull, and arrives at a quite different conclusion concerning the relationship of the vault, face, and cranial base. "It is therefore clear," he states, "from these microcephalic skulls that the dermal bones of the brain case (frontal, parietal, squamosal, supraoccipital) are dependent for their morphological differentiation and growth on the brain, whereas the bones of the skull-base, face and jaws, nasal, maxilla, etc.) are independent of the brain." De Beer, then, would see at least two systems of growth influencing the form of the skull.

Similar conflict of opinion concerning the role of the cranial base in influencing the form of the skull is evident in the divergent statements of Weidenreich and Stockard. Weidenreich ('41, pp. 378-379) states: "The deflection of the base, of course, is of some influence upon the general position of the face but it is not responsible for the degree of prognathism, as Ranke believed, and still less for the reduction of the face." On the other hand, Stockard ('41, p. 282) contends that the cartilaginous growth of the base "functions to produce the bone growth which brings about an almost continuous lengthening of the basi-cranium with the forward development and strengthening of the upper facial skeleton."

These conflicting opinions, based on comparisons of the same types of data, indicate the need for experimental evidence to sort out the

systems of growth in the skull determining the form of the brain case, the face, and the cranial architecture. The experimental method of surgical interference with normal growth has revealed the presence of intrinsic and extrinsic factors during development. Washburn ('47), for example, has demonstrated that certain elements of the skull (temporal lines, nuchal crests, and the coronoid process of the mandible in the rat) develop in direct response to, or are maintained by, muscle function and increasing muscle volume, and are independent of the expansion of the cranial cavity proper.

The vital-staining technique which demonstrates the specific sites of growth also holds an advantage in clarifying problems relating to the ontogenetic development of the skull. While the use of anthropometric techniques has delineated the major proportional changes occurring during the development of the skull, interpretation of the significance of these changes is contingent upon an understanding of the processes of bone growth, the units of growth, and the direction of growth. Thus Keith ('10), Krogman ('31), and Schultz ('40, '41) have described a backward movement of the foramen magnum during the growth of the skull in the gorilla, the chimpanzee, and the orangutan. The causes and the precise mechanisms of the backward migration of the foramen magnum have remained obscure, however, and a full understanding of them must await an analysis of the growth of the base.

Investigators using quantitative anthropometric techniques have been plagued, further, by the problem of superpositioning skull tracings for comparative purposes. That this is a recurrent problem is attested by the fact that Krogman ('51) lists 20 planes which have been suggested at one time or another as a basis for orientation, each attempting to establish an absolute basis of comparison. Adoption of a plane for comparison of different forms or serial tracings of the same form has necessarily depended on the selection of the points in the skull which are assumed to be most stable. The limitations inherent in this method are evident, for commitment to any one plane predetermines the interpretation of differences in dimension, proportion, and the direction of growth and movement in the skull. This problem, as Brodie ('41) has indicated, can be resolved only through the experimental determination of the specific sites of growth.

In the area of growth theory generally, the investigations of Thompson ('17) and Huxley ('32) are cited frequently as having demonstrated the significance of the growth phenomenon as a mechanism of evolu-

tionary change and to account for the differences in form among related groups. Although these writers based their analysis of change of form on the biological nature of the processes of growth, subsequent interest and investigation have tended to focus primarily, and almost exclusively, on the empirical formulations developed by Thompson to show systematic transformations and by Huxley to demonstrate constant differential growth ratios. Huxley's allometric formula ( $Y = bx^k$ ) has been widely applied to describe proportional size shifts during evolution. Robb's ('35) study of the horses and Romer's ('48) study of the Pelycosaurian reptiles may be cited as examples. Simpson ('44) has stated the implications of the concept of relative growth for determining evolutionary rates of change in size of different characters in a phyletic line.

While recognition of the importance of differential growth as a mechanism of evolutionary change has stimulated the development of mathematical techniques for the treatment of dimensional data, little attention has been directed toward the rationale or logical basis for the measurements selected to describe changes in size. Rather, the focus of interest has been directed toward determining general laws of growth inferred from observed regularities in size shifts (i. e., gradients, genetic fields, etc.). The emphasis on application of mathematical techniques has resulted in descriptions of changes in size effecting shifts in form and proportion. This approach does not indicate *how* these changes take place. The utility of inferences about morphological changes derived from a direct application of the mathematical approach without prior consideration of the processes of growth and an analysis of the causal factors involved has been questioned by Waddington ('50), Young ('50), and Washburn ('53).

The solution of problems of morphological change by the technique of mathematical analysis raises the question of the nature of the dimensions selected for study and the basis of selecting these dimensions. Do the measurements submitted to the test of allometric relationship represent measures of discrete morphological elements, functional systems, or units of growth? If the measurements are considered to represent growth changes, then an understanding of growth processes is necessary as a basis of mensuration. This fact has been clearly recognized by Reeve and Huxley ('45) in their discussion of the theoretical basis of the allometric equation and the assumptions concerning the processes of growth on which it rests. Recognizing that bone growth takes place by an additive process rather than one of self-multiplication, these

authors discuss the question of whether the allometric formula can be applied to the analysis of skull growth. Basing their discussion on Brash's ('34) contention that increase in the size of the skull is due to a process of ectocranial apposition and endocranial resorption, Reeve and Huxley ('45, pp. 135-136) state that "an individual skull-bone cannot be considered as a unit of either multiplicative or additive growth," and conclude that "it seems clear that no simple concept of multiplicative or additive growth can be applied to explain changes in skull proportions." This raises a question; namely, to what units of the skull ought the allometric equation be applied in order properly to measure differential growth? The development of an experimental technique designed to demonstrate the processes of bone growth as a logical basis for subsequent mathematical analysis of differential growth and consequent change in the form of the skull would provide a solution of this problem.

In regard to the experimental investigation of the processes of skull growth, little use has been made of the vital-staining technique since John Hunter (1771) described the appositional nature of bone growth in the mandible of madder-fed pigs.

Brash's ('34) analysis of skull growth, also based on madder-fed pigs, led him to the conclusion that the growth of the cranium in size can be explained by surface accretion and surface resorption without any real separating growth at sutural lines. He considered the apparent growth taking place at the sutures as indicating reformation of the sutures required by the expanding surface and designed to maintain the relative position of the suture during increase in cranial size. Although Brash regarded the growth of the cranial base as due to a process of cartilage replacement which resulted in the growth of the bones at the ends (comparable to the growth of long bones), he did not extend his work to include a consideration of the relation of the growth of the cranial base to that of the vault or the influence of growth on cranial form.

Massler and Schour's ('51) study of cranial vault growth in the rat, using the vital-staining technique, does not support Brash's contention concerning the mode of growth in the vault. These authors demonstrate that vault growth takes place by a process of incremental growth at specific sites (sutures). By injecting animals at different ages with a dye which is deposited only in bone growing at that time, they measured the new bone deposited during intervening periods. This method revealed a greater amount and duration of growth at sutures contributing



to growth in length than at sutures resulting in growth in breadth of the vault. Massler and Schour regard the progressive elongation of the cranial vault and snout of the rat as a function of unequal growth at the individual sutures.

Moore ('43) studied the sites of cranial growth in the monkey as revealed by sectioning a single specimen which had been subjected to vital staining with the same dye, alizarin red S. His findings also indicate the suture to be the site of bone deposition responsible for increase in the size of the vault. Although Moore noted the presence of dye on all surfaces as well as in the internal structure of the bones comprising the base, he attributed this staining to a reorganization of the internal structure of the bone.

The project here reported is concerned with the processes of cranial growth as a basis for assessing the influence of differential size increase of the individual units of growth on the form of the skull. To this end, the vital-staining technique used by Massler and Schour to reveal the centers, sites, and mode of growth in the cranial vault was also extended to an analysis of the processes of growth in the face and the base of the skull.

#### MATERIALS AND METHODS

The subjects of this study comprise a series of 77 pure strain albino rats raised in the Physical Anthropology Laboratory of the University of Chicago. Date of birth was recorded for each litter. The animals were weaned at 25 days of age.

The method of vital staining with alizarin red S was used to determine the sites and the extent of new bone formation at different ages. (Alizarin is deposited in the new bone being calcified at the time of injection, while bone formed prior to the injection or subsequent to the period of absorption of the stain remains white.) A 2% solution of alizarin red S with a dosage of 1 cc per 100 gms of body weight was administered by intraperitoneal injection or, in very young animals, by subcutaneous injection between the scapulae. With the older animals, since the rate of bone deposition has slowed down, injection of alizarin red in full dosage on two successive days was found to be more effective in producing a deep, rich stain.

The animals were injected at varying ages in order to provide a representative series from birth to 101 days of age. The distribution of animals by sex, age injected, and age sacrificed is shown in table 1.

TABLE 1

*Distribution of animals by sex, age alizarinated, and age sacrificed*

ALIZARIN AGE (days)	SACRIFICED AGE (days)	NUMBER		ALIZARIN AGE (days)	SACRIFICED AGE (days)	NUMBER	
		M	F			M	F
1	4	1	1	26,28	90	-	1
1	5	1	-	26,28	100	-	1
1	7	1	-				
1	9	1	-	27,29	50	1	-
1	10	1	-	27,29	55	1	-
1	15	1	-	27,29	60	-	1
1	20	-	1	27,29	65	1	-
6	10	-	1	27,29	70	-	1
6	13	1	-	27,29	75	1	-
				27,29	80	-	1
10	15	3	-	27,29	85	-	1
10	16	1	-	27,29	90	-	1
10	20	3	-	27,29	97	-	1
10	25	2	-	27,29	101	-	1
10	28	1	-				
10	30	-	1	31,32	35	1	-
10	35	1	-	31,32	38	-	1
				31,32	41	1	-
15	17	1	-				
15	25	1	-	35	36	1	-
15	30	1	-	35,36	45	1	-
15	35	1	-				
15	40	-	1	40,41	45	1	-
				40,41	50	1	-
18	25	-	1	40,41	55	1	-
20	25	1	1	45,46	50	-	1
20	28	1	-	45,46	55	-	1
20	30	1	-	45,46	60	1	-
20	35	1	1				
20	45	-	1	50,51	55	1	-
				50,51	60	-	1
25,26	29	1	-	50,51	65	1	-
25,26	32	-	1				
25,26	35	1	-	55,56	60	1	-
				55,56	65	1	-
26,28	50	-	1	55,56	70	1	-
26,28	60	1	-				
26,28	65	1	-	70,71	76	-	1
26,28	70	1	-	70,71	83	-	1
26,28	80	-	1	70,71	97	1	-
				70,71	100	1	-

Total 50 27

Total N = 77

Termination of the series at 101 days of age for the oldest animal was decided upon, since it was evident from a cursory examination of the specimens that this period of time covered the major growth changes taking place in the skull of the rat.

The maceration of the specimens was greatly facilitated by soaking them briefly in a solution of one part commercial household bleach containing sodium hypochlorite to two parts of water. No specimen was left in the solution for more than 5 minutes at a time. Cleaned specimens were then rinsed in three or 4 changes of clear water and stored in a dilute solution of alcohol.

The method of analysis consisted of making qualitative observations, on the articulated skulls, of the growth centers and the sites of growth active at different ages. The mode or process of growth (i. e., surface apposition or incremental addition at the margins of the center of ossification) at the different sites of bone deposition was determined. The direction of incremental growth as revealed by the staining technique was the basis for metrical assessment. Since the sites of bone growth were known, it was possible to devise measurements at right angles to the plane of growth. The measurements reported represent diameters of whole bones. Length and height measurements were taken in the midsagittal plane, breadth measurements at the widest part of the bone.

Methodologically, the question arises: does the use of alizarin red S interfere with the normal growth of the animals, and thus make them undesirable subjects for the quantitative aspects of the study? This problem is further complicated by the age differential at time of injection and the possibility that animals react differently according to when, during the period of growth, the dye is introduced. While experimental physiological data are not available, it was observed that no animal remained ill, as the apparent result of the injection, for longer than 24 hours. Nor did younger animals appear to be more susceptible than older ones to the slightly toxic effect of the stain.

## FINDINGS

### *Centers, Sites, and Modes of Growth Resulting in Dimensional Changes in the Skull*

*The Occipital Complex.* The occipital bone of the rat at birth consists of 4 elements, each represented by a single center of growth: the basioccipital, the paired exoccipitals, and the supraoccipital. These

elements are arranged in two planes. The basioccipital forms the posterior floor of the brain case; the exoccipitals and the supraoccipital, the back wall of the cranial cavity.

The basioccipital increases in length and breadth by incremental growth at the margins, with the exception of the posterior margin forming the ventral border of the foramen magnum. Stained specimens show clearly a continuous increment of new bone formation extending the anterior and lateral margins of the element (fig. 1).

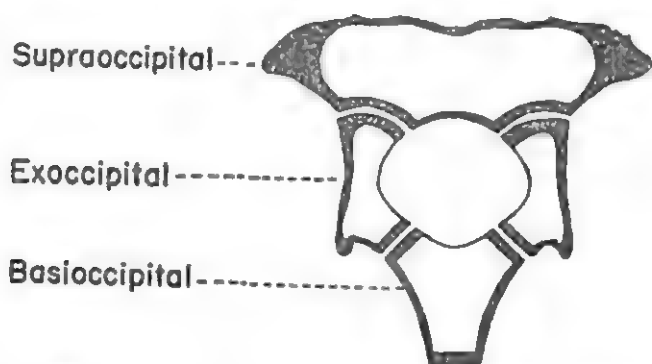


FIG. 1. SCHEMATIC DIAGRAM ILLUSTRATING RELATIONSHIP OF GROWTH SITES OF OCCIPITAL ELEMENTS TO THE FORAMEN MAGNUM IN 20-DAY-OLD RAT. (Shaded areas represent growth from 10th to 20th day; basioccipital arranged in vertical plane for diagrammatic simplicity.)

There is no indication of bone deposition suggesting incremental increase at the posterior margin of the basioccipital (and thus at basion) at any time during the 101-day period represented by this series.

Growth in length of the basioccipital takes place at the synchondrosis formed with the basisphenoid. Since the junctions of the basioccipital with the exoccipitals are set at angles to the midsagittal plane of the skull, the incremental growth at these sites contributes to increase in both length and breadth of the basioccipital.

The lateral margins of the basioccipital abutting the tympanic bullae show incremental increase without preformation in cartilage. This mechanism of increasing the lateral diameter is unlike the growth of long bones in breadth resulting from surface apposition. The surfaces (ectocranial and endocranial) of the basioccipital, after injection, are lightly stained red, indicating appositional growth resulting in an increase in thickness of the bone. The unstained band of new bone



surrounding the area of stained surface indicates clearly that the lateral dimension does not increase by surface apposition.

The distribution of the stain shows that the exoccipitals, with the exception of the medial margins comprising the lateral borders of the foramen magnum, increase in height and width by incremental growth at the margins of the growth center (fig. 1). Growth occurs at the junctions of the exoccipitals with the basioccipital and the supraoccipital as a result of endochondral bone formation, whereas the lateral margins meeting the periotic capsules show incremental growth without preformation in cartilage.

The supraoccipital also increases in dimension by incremental addition at the margins of the single center of growth. Unlike the other elements of the occipital bone, the ventral margin of the supraoccipital forming the superior border of the foramen magnum shows a "filling in" suggestive of incremental increase contributing to its vertical dimension. As compared with the nature of the staining at the other margins, however, this incremental growth is not sharply defined. While it does contribute to the vertical height of the supraoccipital in the midline, the chief effect appears to be the flattening of the superior margin of the foramen magnum during growth.

Since the elements of the occipital bone are arranged roughly in two planes, the growth sites described result in the expansion of the occiput in height, length, and breadth. While the borders of the foramen magnum undergo lipping and increase in thickness during the period studied, the pattern of staining in specimens permitted to survive for some time after injection demonstrates that incremental growth does not take place at the lateral or inferior margins of the foramen magnum. The amount of growth at the sites joining the 4 elements of the occipital determines and controls the size of the foramen magnum, as illustrated in figure 1.

*The Cranial Base.* The basioccipital has been discussed in connection with the growth of the occiput. The sphenoid bone in the rat forms the central part of the floor of the brain case and the lower part of the lateral walls. The basisphenoid grows in length by incremental addition at the synchondroses present at the anterior and posterior ends of the bone (fig. 2). The surface of the bone forming at the time of absorption of the stain shows a pink coloring, owing to surface apposition causing increase in thickness of the bone. Since the lateral margins of the basilar part of the sphenoid do not show a concentration of stain indi-

cating sites of incremental growth, as in the basioccipital, it is evident that increase in lateral dimension is attained by surface apposition, as in a long bone.

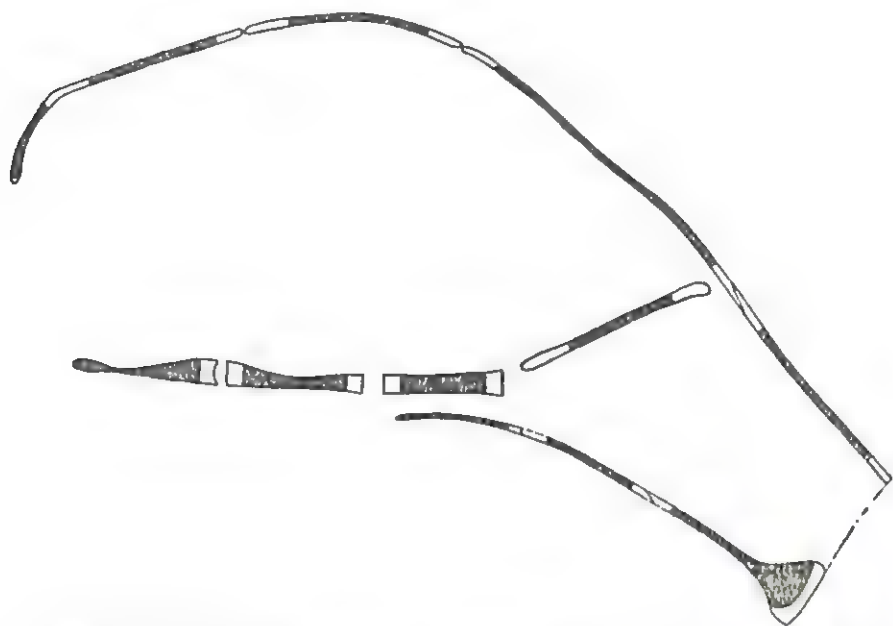


FIG. 2. SCHEMATIC DIAGRAM OF THE MIDSAGITTAL SECTION OF A RAT INJECTED AT ONE DAY OF AGE AND SACRIFICED AT TEN DAYS OF AGE SHOWING: (1) SITES OF GROWTH CONTRIBUTING TO THE INCREASE OF THE SKULL IN LENGTH AND HEIGHT; (2) NEW BONE (WHITE) FORMED SUBSEQUENT TO THE ABSORPTION OF ALIZARIN.

Lateral to the basilar part, the wings of the sphenoid show incremental growth at the margins forming sutures with the squamosals, the frontals, and the presphenoid, contributing to the growth of the bone in width and length. The unattached posterior margins of the wings bordering the petrotympanic fissures are sites of incremental growth also, resulting in increase in length of the pterygoid fossae and the wings of the sphenoid. The anterior ends of the pterygoid processes buttressing the maxillary tubercles show a concentration of stain and increments of new bone deposition, indicating that growth takes place by addition of bone at the anterior ends.

The presphenoid bone forms the anterior part of the floor of the brain case. The basal portion of the presphenoid grows in length by incremental addition of bone at the synchondroses formed with the

basisphenoid posteriorly and the junction with the ethmoid anteriorly (fig. 2). The wings of the presphenoid housing the optic foramina increase in size by incremental growth at the sutures.

*The Lateral Aspect of the Brain Case.* The squamosal bones are arranged in the vertical plane and form part of the lateral walls of the brain case. The distribution of the stain indicates that growth is effected through incremental addition at the sutural margins around a single center of growth. The free posteroventral margin bordering the postglenoid foramen is also indicated as a site of incremental growth. Since the squamosals are situated in a vertical plane, this growth increases the length and height of the brain case.

The paired frontal bones contribute to the formation of both the brain case and the face. Each bone, while developing from a single center of growth, is arranged in several planes and contributes to the dimensional increase of the skull in length, breadth, and height (fig. 2). The posterior part of the frontals meets in the midline dorsally and encircles the anterior end of the brain to join the presphenoid ventrally. Laterally and ventrally the frontals grow in length and height by incremental addition at the margins of the frontosquamosal and frontopresphenoid sutures. Ventrally, incremental growth at the sphenofrontal suture results in dimensional increase of the brain case in length and height.

At the anterolateral margins, the frontals form sutures with the maxillary bones. Incremental growth at the frontomaxillary sutures, as revealed by the pattern of staining, results in dimensional increase in both length and height of the face, since these sutures are arranged at an angle that slopes upward anteriorly in relation to the horizontal. (The growth of the dorsal aspect of the frontal bones has been described by Schour and Massler ('51) in connection with the sites of growth in the cranial vault.)

*Sites of Growth in the Face.* The maxillary bones form the lateral aspect of the face of the rat and house the molar dentition. The maxillae grow in length by incremental addition at the maxillopremaxillary sutures and at the maxillary tubercles at the posterior end of the tooth row. Growth at the latter site results in the lengthening of the alveolar portion of the maxilla housing the upper molars. Incremental growth at the frontomaxillary sutures contributes to increase in height of the body of the maxillary bones.

Ventrally, the maxillae form the anterior portion of the hard palate. Incremental growth at the margins of the intermaxillary suture results in a widening of the palate and separation of the parallel tooth rows formed by the upper molars.

The anterior half of the zygomatic arch is part of the maxillary bone in the rat. The stained specimens indicate clearly that the zygomatic arch grows by a process of surface apposition on the superolateral margin and bone resorption from the inferomedial aspect of the arch. This process of apposition of layers of bone on the outer aspect, with removal of old bone on the medial aspect, results in movement of the arch laterally and in increase in size of the temporal fossa. The mechanism of dimensional increase of the bizygomatic diameter results in the continuous replacement of bone tissue and in the structure of the arch itself, as compared with the mode of incremental growth which enlarges a bone by adding to it at its margins.

The zygomatic bones forming the central part of the arches also grow laterally, owing to apposition on the lateral surfaces and resorption from the medial surfaces. The same process is evident at the posterior root of the arch formed by extensions from the squamosae. The overlapping sutural junctions formed by the zygomatic bones with the anterior (maxillary) and posterior (squamosal) roots of the arch show increments of new bone formed subsequent to injection of the stain. This incremental growth results in longitudinal growth of the arches in keeping with the growth of the cranium in length.

The premaxillary bones form the anterior portion of the snout laterally and ventrally and border the nasal bones along the dorsal aspect of the snout. Each bone develops from a single center of growth. The premaxillae house the upper incisor teeth of the rat.

The premaxillae increase in size by both incremental and surface appositional modes of growth. Growth in length takes place by incremental addition at the maxillopremaxillary sutures, at the free anterior margins bordering the nasal aperture, and at the lateral edges of alveolar bone bordering the incisors. Growth in length of the premaxillae also takes place at the frontopremaxillary sutures by incremental addition. The pattern of staining also reveals incremental growth at the interpremaxillary suture on the ventral aspect of the snout, contributing to growth in the lateral dimension.

Increase in vertical dimension, however, takes place by surface apposition on the dorsal aspect of the premaxillae bordering the nasal bones



and by incremental growth at the free anterior margin of the premaxillae ventral to the nasals. No incremental growth of the premaxillae, at the nasopremaxillary junction, is evident during the 101-day period represented by this series. The mode of surface appositional growth is clearly evident in the comparison of two animals injected at the same age but sacrificed at different ages. An animal sacrificed a few days after injection shows red stain over the surface of the premaxillae bordering the nasal bones, while one sacrificed after some time exhibits a surface of white bone covering the stained surface laid down previously.

*Growth of the Cranial Vault.* Massler and Schour ('51) have reported on the centers, sites, and modes of growth of the paired nasals, frontals, parietals, and the interparietal that comprise the cranial vault in the rat. They demonstrated that growth of the vault takes place by incremental addition at the sutural margins around the centers of growth. This pattern of dimensional increase is confirmed by the animals of this series, as shown in figure 2.

Massler ('41) also demonstrated that the amount of growth is not always equal on the two sides of the suture. He showed that the parietals sustain a greater increment of growth than the interparietal at the parietointerparietal suture (Massler's anterior lambdoid suture). This phenomenon also has been observed in the animals of this series.

*Growth of the Mandible.* The pattern of staining indicates that the posterior and superior borders of the ramus comprise a continuous site of growth, largely responsible for the dimensional increase of the mandible in length and height. Stained specimens show a sharp increment of new bone extending along these margins, and including both the angle of the mandible and the anterior aspect of the tip of the coronoid process. The anterior margin of the ramus and the inferior border of the ramus do not represent sites of growth contributing to the dimensional increase of the mandible.

The addition of new bone at the tip of the coronoid process and along the superior margin of the ramus does not alter the backward angulation of the anterior border during the growth of the mandible. The fact that the stain reveals the old contours of the coronoid process in animals sacrificed as many as 30 days subsequent to injection indicates that the anterior margin of the ramus is not subject to resorption. The incremental growth at the angle of the mandible results both in backward and downward extension of the ramus as the mandible grows in length.

Growth in height of the body of the mandible is related to the specialized dentition of the rat, and since the incisors extend along the entire ventral aspect of the body of the mandible, surface appositional growth of the alveolar bone contributes to this growth in height. So also does the incremental addition of new alveolar bone, which progresses in conjunction with the eruption of the molars. The continuous eruption of the incisors is accompanied by incremental growth at the anterior margin of the body of the mandible, thereby contributing to the growth in length of the mandible. Except for the special nature and requirements of the rat's dental apparatus, the growth of the mandible in the rat is essentially comparable in pattern to the growth of the mandible of the pig reported by Brash.

The sites of growth in the midsagittal plane described as contributing to increase in height and length of the skull are illustrated in figure 2.

*Sites of Bone Deposition and Resorption Resulting in Changes in the Cranial Architecture of the Rat*

Analysis of animals injected and sacrificed at different ages reveals the presence of sites of bone deposition and resorption concerned primarily with changes in the architecture and proportions of the skull, rather than with dimensional increase of individual bones. These sites are therefore distinguished from those responsible for growth in size per se and are described separately.

*Differential Growth of the Cortical Plates of the Vault Bones.* The stained animals of this series reveal that the sutures of the cranial vault represent sites of differential growth related to changes in cranial form. The vault of the rat, rounded at birth, undergoes progressive longitudinal flattening in conjunction with growth in size. As a result, the bones of the dorsal aspect of the vault are rearranged in the horizontal plane and form almost a right angle with the supraoccipital, which is nearly vertical in orientation.

The examination of disarticulated specimens shows unequal growth of the inner and outer tables of the same bone at the sutural margin. The difference in increment of new bone formation is evident by direct comparison of the outer and inner tables of the paired bones of the vault. Beginning at 10 days of age, differential growth results in the outer table of one bone overlapping the inner table of the adjoining bone at the sutural junction. A slight incremental growth at the edges of some

of the cortical plates was noted throughout the time span covered by this series. Animals sacrificed after injection at 70 and 71 days of age showed particularly a new increment of growth at the posterior margin of the outer plate of the parietals and at the anterior margin of the inner plate of the interparietal.

The pattern of staining on the ectocranial and endocranial surfaces of the vault, examined under low-power magnification, indicates that differential surface apposition and resorption are not the mechanism responsible for the longitudinal flattening of the dorsal aspect of the cranium. The surfaces of the vault show the greatest concentration of stain near the sutural margins and less intense staining in the central areas. The same pattern of staining is found both in animals sacrificed only two days after injection and in those permitted to survive as long as 70 days after injection. The pink stain in the center area of the bone results from an increase in thickness of the bone due to surface apposition. The deeper staining near the sutural margins results from both surface apposition and incremental growth at the sutural margins.

These findings, in the rat, do not support Weinmann and Sicher's ('47) statement that the cranial vault bones flatten out during growth as a result of apposition on the endocranial surface in the central areas of the bones and resorption of the endocranial surface near the sutural margins.

*Changes in the Internal Architecture of the Basioccipital Element.* Examination of the surfaces and internal structure of the basioccipital element in stained specimens indicates extensive remodeling concurrent to growth in size. At approximately 15 days of age, a median ridge is formed on the ventral aspect by surface apposition. By 20 days of age there is evident resorption of bone on both sides of the median ridge posterior to the area of insertion of the longus capitis muscles near the synchondrosis. The combined processes of deposition and resorption result in the formation of troughlike depressions on either side of the median ridge, giving the lateral margins of the basioccipital a raised appearance. Anterior to the area of resorption, surface deposition results in an increased thickness of the bone near the synchondrosis. The continuing process of deposition at the anterior end of the bone, followed by resorption, results in a thinning of the body of the basioccipital which makes the bone translucent. Surface remodeling is accompanied by changes in the trabeculae, as indicated by continued staining of the internal structure at the base of the median ridge.

The changes in the structure of the basioccipital, involving both continuous deposition and resorption of bone, are related to factors of muscle tension and reduction in bone mass, and are independent of dimensional growth.

### *Quantitative Growth of the Skull*

The sites and processes of growth described in the preceding section indicate that dimensional increase of the skull is the result of incremental addition at the borders of each center of ossification. At birth the bones in the rat skull, with the exception of the occipital complex, each comprise a single osseous unit. The individual bone, therefore, is the logical unit of study in analyzing the dimensional and proportional changes occurring during growth.

Since a mathematical analysis of growth rates determining cranial form is not the purpose of this paper, the effect of differential growth of individual bones is chiefly demonstrated graphically.

Measurements of the bones comprising the brain case and of the frontal and nasal bones in the face were taken on all specimens in the series, even though the absence of stain suggested earlier cessation of growth at specific sites. This procedure makes possible a comparison of the duration of growth as determined by qualitative and quantitative methods.

*Differential Growth Rates: Curves of relative growth.* To determine the phases of relative growth rates (increase in millimeters per unit time per millimeter), it is expedient to plot the measurements on semi-logarithmic paper. The mean values of the measurements, grouped by 5-day intervals, are shown in figure 3.

The period of most rapid postnatal growth for all dimensions studied occurs during the first 20 days after birth, as shown by the slope of the curves. The 11 dimensions show in common an inflection between 15 and 20 days, indicating a decrease in relative rate of growth at this time. After the inflection the relative growth rates are much reduced. The greater slopes of the relative growth curves before the inflection period correspond to the accelerating phase of absolute growth completed by 20 days of age.

The relative growth rates are not constant for any considerable period of the total time during which the dimensions were studied. Although segments of each curve may be approximated by a straight line, suggesting that for short periods relative growth adheres to an exponential



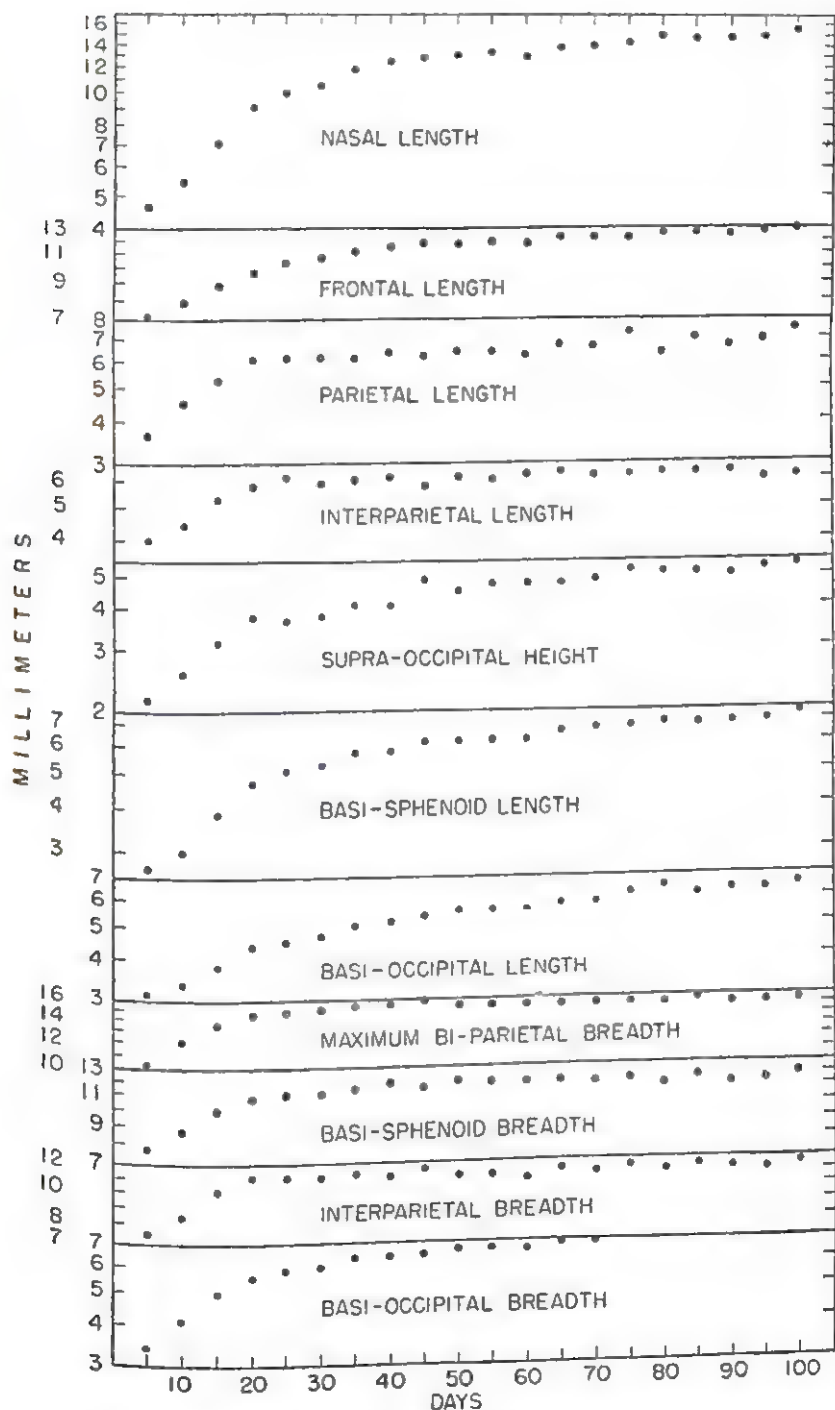


FIG. 3. RELATIVE GROWTH CURVES OF INDIVIDUAL BONES IN SKULL OF THE RAT. NOTE THE INFLECTION PERIOD AT 15-20 DAYS OCCURRING IN THE LOGARITHMIC PLOTTING OF ALL DIMENSIONS STUDIED.

formula, the complete curves show breaks indicating successive changes in rate of deceleration.

*Curves of absolute growth.* Absolute growth curves are shown in figures 4, 5, and 6. The decelerating phase of the curves was fitted by

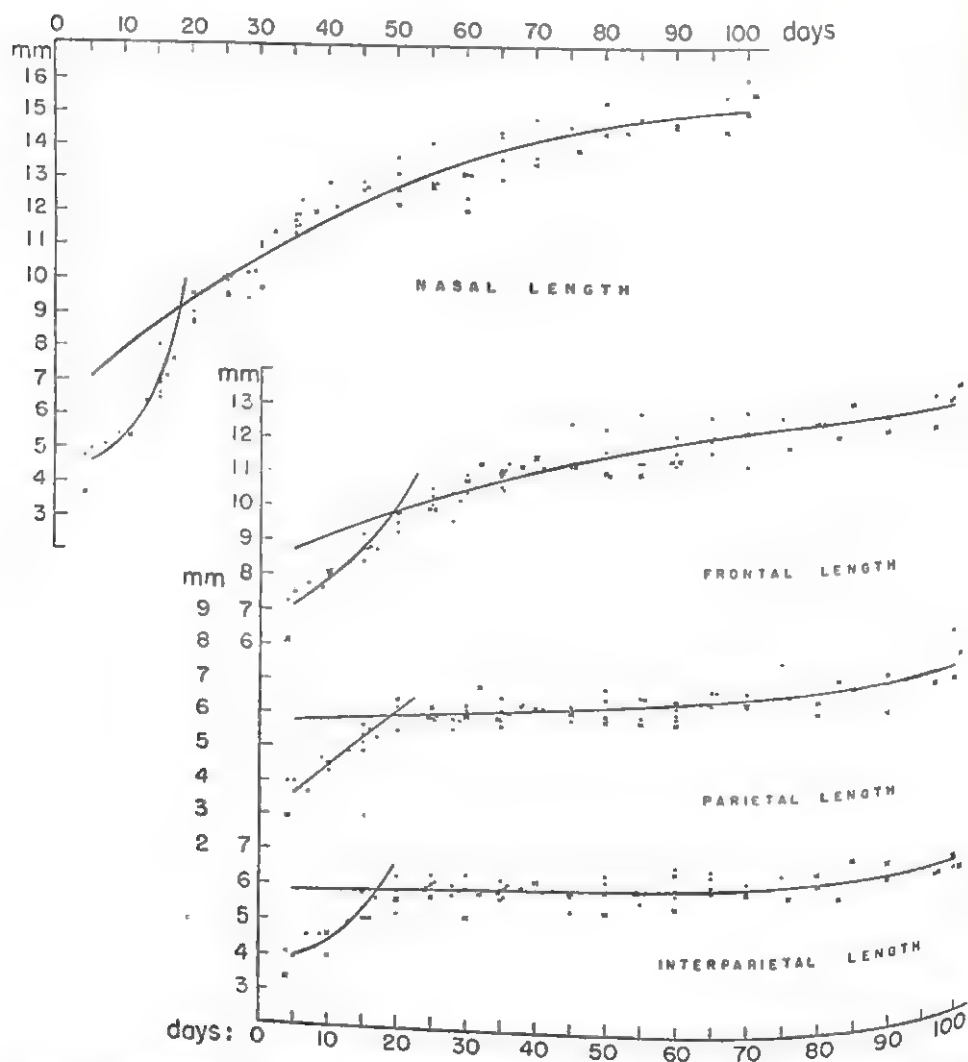


FIG. 4. ABSOLUTE GROWTH CURVES, SHOWING GROWTH IN LENGTH OF INDIVIDUAL BONES COMPRISING DORSAL ASPECT OF SKULL OF THE RAT (dot, male;  $\times$ , female).

the method of orthogonal polynomials described by Snedecor ('46). To do so the data were grouped in 5-day intervals. The curves relate to the growth of the cranial vault and the cranial base respectively.

*Dimensional change in the dorsal aspect of the skull*

*Growth in length of the individual bones.* The staining at the sites of growth contributing to increase in length of the cranium and the dorsal aspect of the face indicates growth throughout the first 100 days of postnatal life. Continued deposition of very small increments of new bone is visible in animals injected at 70-71 days of age and sacrificed at successive periods up to 100 days.

Differences in the amount of growth and pattern of deceleration of the individual lengths is revealed in a comparison of the curves. At the 1% level of significance the interparietal and parietal lengths are best fitted by a first degree curve (a straight line), while the nasal and frontal lengths are fitted by a second degree curve (a segment of a parabolic arc). These curves (fig. 4) demonstrate the contrast in the rates of growth of the interparietal and parietal on the one hand, and the frontal and nasal lengths on the other. Specifically, the interparietal and parietal bones show rapid deceleration during the period of inflection, followed by constant, slow linear growth. The frontal and nasal bones show a much longer period of slow deceleration. Expressed in terms of size attained at 100 days of age, the interparietal reaches 85% of total length at 15-20 days, the parietals at 25 days, the frontals at 30-35 days, and the nasals at 50-55 days of age.

Comparison of the calculated attainments of the individual bones shows an incremental gradient of growth in the dorsal aspect of the skull. From the interparietal bone forward, each bone shows successively a greater total amount of growth at 100 days. (The length at 5 days of age, the increments of growth by 25-day periods, and the length at 100 days of age are listed for each bone in table 2.) The absolute size attained by each of the bones is related, not to the size at 5 days of age, but rather to the position of the bone in the skull.

TABLE 2

*Incremental growth of bones in the dorsal aspect of the skull (mm)*

	NASAL LENGTH	FRONTAL LENGTH	PARIETAL LENGTH	INTERPARIETAL LENGTH
Length at 5 days	4.60	7.14	3.62	3.99
Increase 5-25 days	5.49	3.11	2.44	1.93
Increase 26-50 days	2.72	1.39	.36	.13
Increase 51-75 days	1.60	.82	.35	.12
Increase 76-100 days	.65	.25	.35	.12
Total increment (5-100 days)	10.55	5.57	3.50	2.30
Length at 100 days	15.15	12.71	7.12	6.29
Increase over size at 5 days (per cent)	229.6	78.0	96.7	57.7

*Growth in breadth of the interparietal and parietal bones.* For this series, deposition of bone at the sites of growth contributing to increase in width of the parietals is revealed by the stain until 30 days of age. Measurement of biparietal width, however, indicates rapid deceleration until 35 days of age; after this time

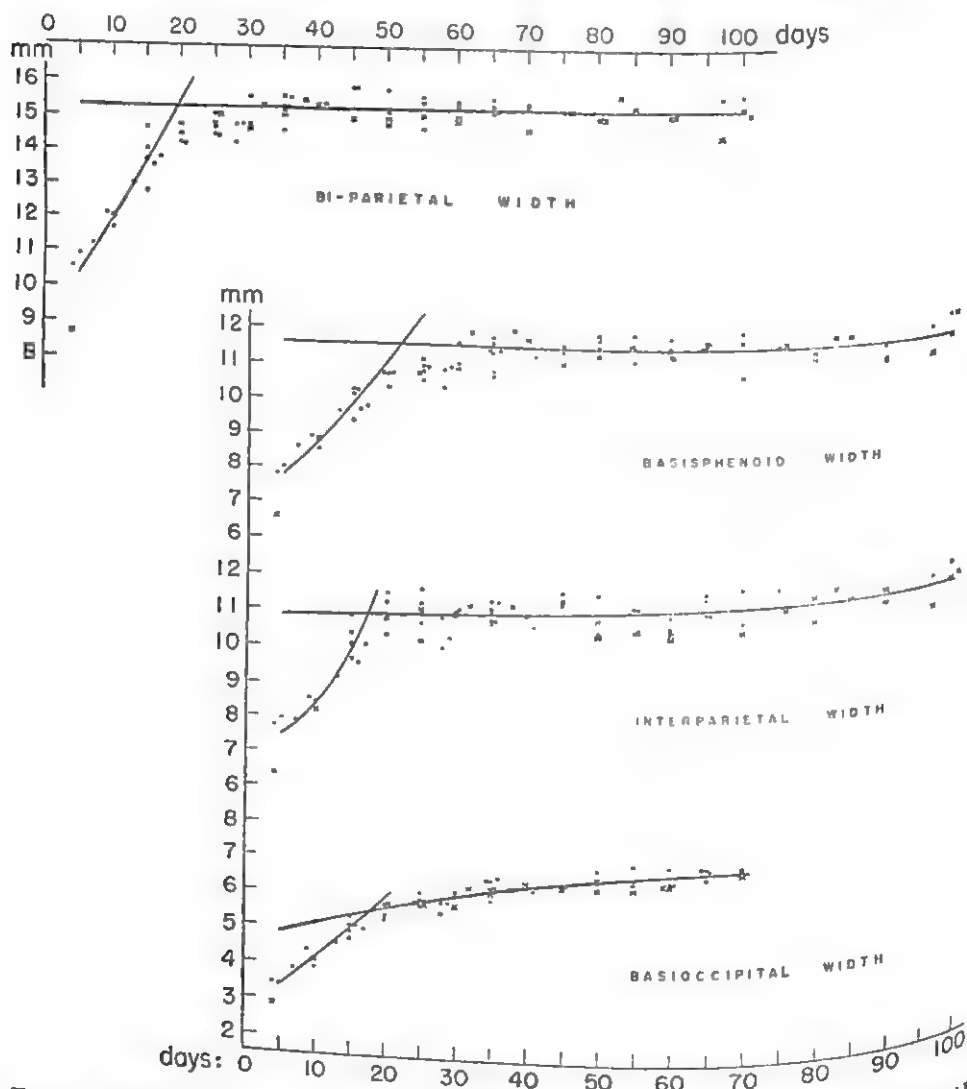


FIG. 5. ABSOLUTE GROWTH CURVES, SHOWING GROWTH IN WIDTH OF INDIVIDUAL BONES COMPRISING VAULT AND BASE OF SKULL OF THE RAT (dot, male;  $\times$ , female).

there is no significant dimensional increase (fig. 5). Of the total biparietal width 85% is achieved by 10-15 days of age. The presence of stained bone shows that interparietal breadth increases throughout the period studied. The curve of growth illustrates rapid deceleration during the inflection period and slow linear



growth through 100 days of age (fig. 5). The biparietal and interparietal widths at 100 days show an increase in size over that at 5 days of age by 48.2% and 52.9%, respectively.

*Dimensional change in the cranial base.* The measurements of the base here reported concern the growth of the presphenoid, basisphenoid, and basioccipital bones. The length of the presphenoid bone could not be determined for most of the series, since to do so would have necessitated disarticulating each specimen. Description of the growth of the presphenoid, therefore, is based on the values obtained from 6 sectioned skulls.

*Growth in length of the individual bones.* All sites of growth described as contributing to increase in base length show deposition of new bone throughout the period studied. The measurements of basioccipital and basisphenoid length comprise second degree curves, characterized by a long period of slow deceleration (fig. 6). The plotted values of presphenoid length for the 6 sectioned skulls indicate a pattern of growth similar to that of the other bones in the base.

Comparison of the total increment of growth for each of the bones of the base indicates that the greatest absolute gain in length occurs in the basisphenoid. In terms of percentage increase over size at 5 days of age, however, the greatest relative increase occurs in the presphenoid; it is successively less for the basisphenoid and the basioccipital (table 3).

TABLE 3

*Growth of the bones of the cranial base (mm)*

	PRESPHENOID LENGTH *	BASISPHENOID LENGTH	BASIOCCIPITAL LENGTH
Length at 5 days	2.52	2.71	3.16
Length at 100 days	6.72	7.07	6.46
Total increment	4.20	4.36	3.30
Increase over size at 5 days (per cent)	166.7	160.9	104.4

\* Total values based on 97 days of age.

*Growth in breadth of the basisphenoid and basioccipital bones.* The presence of stained bone along the sphenoidal margins of the sphenosquamosal sutures in animals injected at varying ages is evidence of the continued growth in width of the basisphenoid throughout the period studied. The curve of growth, however, indicates no significant dimensional increase after approximately 35 days of age (fig. 5).

The basioccipital element shows deposition of new bone along the lateral margins through 100 days of age. Union of the basioccipital with the exoccipital elements begins at 50 days of age and is completed by 70 days, when the junction becomes difficult to detect. Measurement of basioccipital width was therefore

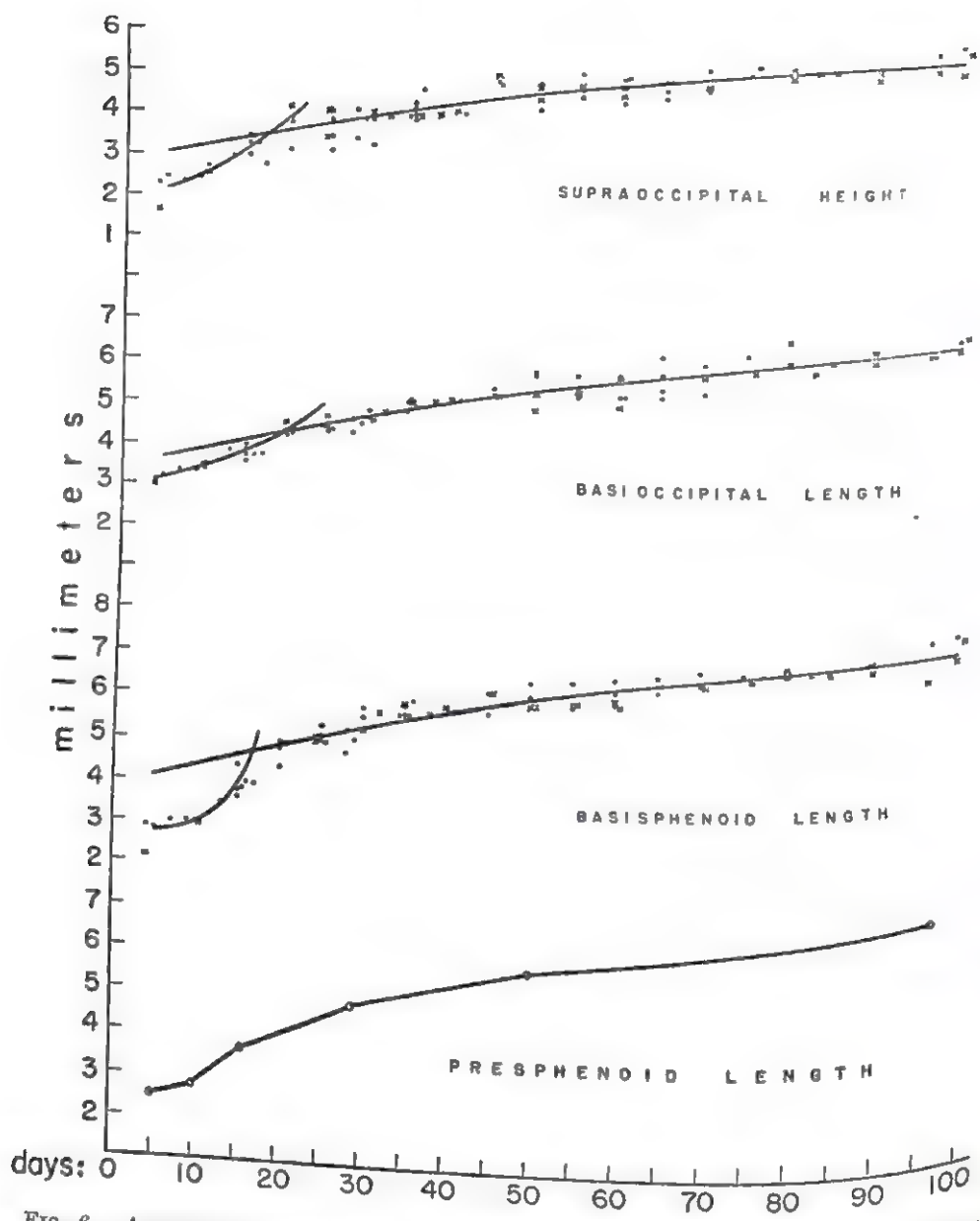


FIG. 6. ABSOLUTE GROWTH CURVES, SHOWING GROWTH IN LENGTH OF INDIVIDUAL BONES COMPRISING BASE AND OCCIPUT OF SKULL OF THE RAT (dot, male;  $\times$ , female).

attempted only through the 70th day. After the accelerating phase of growth, maximum basioccipital width is fitted by a second degree curve, characterizing slow deceleration (fig. 5).

*Growth in height of the occiput.* Increase in the height of the occiput occurs as the result of incremental growth at the exoccipital-supraoccipital junctions and at the supraoccipital-interparietal suture. The exoccipital elements begin to unite with the supraoccipital at approximately 45 days, and fusion is completed by 60 days of age, when the occipital complex comprises a single bone. Subsequent increase in height of the occiput results from the slow, continued deposition of bone at the superior margin of the supraoccipital through 100 days of age.

Measurements of supraoccipital height, taken in the midsagittal plane, are fitted by a second degree curve (fig. 6). The dimensional increase of supraoccipital height is similar in pattern to that described for the bones of the base; and, as with the bones of the base, approximately 85% of the total size is achieved at 50 days of age. The total size attained by the supraoccipital represents an increase of 143.8% over the size at 5 days of age (compare table 3).

*Sex Differences.* Mean deviations of males and females from the computed values for the total series at 5-days intervals were determined for each of the dimensions studied. For the length dimensions of the skull, the observed differences between males and females in these dimensions are not significant at the 5% level during the first 100 days of postnatal life.

In the breadth of the skull, however, test of the mean deviations indicates that differences as great as those observed might occur as a result of sampling fluctuation alone only 2% of the time for basioccipital width and only 1% of the time for biparietal and interparietal widths.

Mean deviations, "t" values, and probability (p) of chance occurrence of sex differences are listed in table 4.

*Quantitative Growth of the Skull: Summary.* The individual bones of the rat skull grow most rapidly during the first 20 days of postnatal life. After the accelerating phase the bones of the dorsal aspect of the skull show two dissimilar patterns of growth in length; that is, the parietals and the interparietals undergo rapid deceleration, followed by slow linear growth, while the nasals and the frontals maintain a pattern of slow deceleration resulting in greater dimensional increase. In contrast to the vault and face, the bones in the base of the skull exhibit a single pattern of decelerating growth.

Comparison of dimensional growth in length reveals that the bones of the base undergo a greater relative increase than do the bones of the dorsal aspect of the skull, with the one exception of the nasal bones.

TABLE 4

*Test for sex differences of the rat skull*

LENGTH DIMENSIONS	NUMBER		MEAN DEVIATION		DIFFERENCES M AND F (mm)	<i>t</i>	<i>p</i>
	M	F	M	F			
Nasal	50	27	.0648	— .1463	.2111	1.587	.11
Frontal	50	27	.0398	— .1115	.1513	1.528	.13
Parietal	50	27	.0436	— .0985	.1421	1.712	.09
Interparietal	50	27	.0542	— .0863	.1405	1.925	.06
Supraoccipital	50	27	— .0064	— .0607	.0543	.835	.41
Basioccipital	50	27	— .0020	— .0204	.0184	.354	.73
Basisphenoid	50	27	.0442	— .0689	.1131	1.984	.05
BREADTH DIMENSIONS							
Biparietal	50	27	.0838	— .1641	.2479	2.666	.01
Interparietal	50	27	.0752	— .1800	.2552	2.604	.01
Basioccipital	47	17	.0387	— .1024	.1411	2.352	.02
Basisphenoid	50	27	.0330	— .0348	.0678	.779	.44

Growth in breadth of the skull at the maximum widths of the parietals and the basisphenoid shows rapid deceleration and completion at approximately 35 days of age. The growth in width of the posterior part of the skull, however, continues through the first 100 days of life. During the decelerating phase the pattern of growth in width of the dorsal aspect of the skull is slightly different from that of the base, since interparietal width decelerates more rapidly than basioccipital width. The height of the occiput shows a pattern of dimensional increase similar to that of the base, with growth continuing through 100 days of age.

These data are in agreement with the basic growth pattern described for the vault of the rat by Massler and Schour ('51). The chief differences pertain to the time of cessation of growth; the findings here reported suggest longer duration of growth at the sites responsible for increase in length of the skull and height of the occiput.

Measurement of individual bones, based on the sites of growth, indicates the presence of different patterns of dimensional increase determining proportional changes in the skull.



*Proportional Changes in the Dorsal Aspect of the Skull*

The dorsal aspect of the skull exhibits two major changes in proportion resulting from differential growth of the individual bones, namely: (1) reduction in the relative length of the cranial vault in comparison with the length of the face and (2) reduction in the relative width of the skull.

*Changes in Craniofacial Proportions.* The dorsal aspect of the cranial vault is composed of the interparietal and parietal bones and the posterior part of the frontals; the dorsal aspect of the face consists of the anterior part of the frontal bones and the nasal bones. The junction of cranium and face at the posterior margin of the frontal sinuses is marked ectocranially by a transverse depression and endocranially by a ridge of bone.

TABLE 5

*Relative length of the individual bones in dorsal aspect of skull  
(percentage of total skull length)*

DAYS	NASAL	FRONTAL	PARIETAL	INTERPARIETAL	TOTAL SKULL
5	23.77	36.90	18.71	20.62	100.00
10	24.30	35.57	20.25	19.88	100.00
15	26.76	33.21	19.98	20.05	100.00
30	32.12	31.68	18.37	17.83	100.00
50	34.70	31.54	17.37	16.39	100.00
70	36.13	31.31	16.98	15.58	100.00
100	36.71	30.80	17.25	15.24	100.00

The sequential change in craniofacial proportions is demonstrated by a comparison of the relative size of the individual bones. Table 5 shows the percentage of total skull length contributed by each of the bones at different ages. The pattern of change is shown graphically in figure 7.

The first 15 days of postnatal life are the period of greatest relative size of the cranial vault (fig. 8-B). During this time the parietal bones show a small increase in relative size, while the interparietal remains essentially unchanged. Although the cranial portion of the frontal bones grows in conjunction with the vault, the total bone undergoes a

marked decrease in relative length, owing to the comparatively slow growth at the frontonasal suture. The nasal bones show an increase of only 3% of total skull length from 5 through 15 days of age.

After 15 days of age, however, there is a shift in trend, resulting in a progressive increase in relative face length over cranial length.

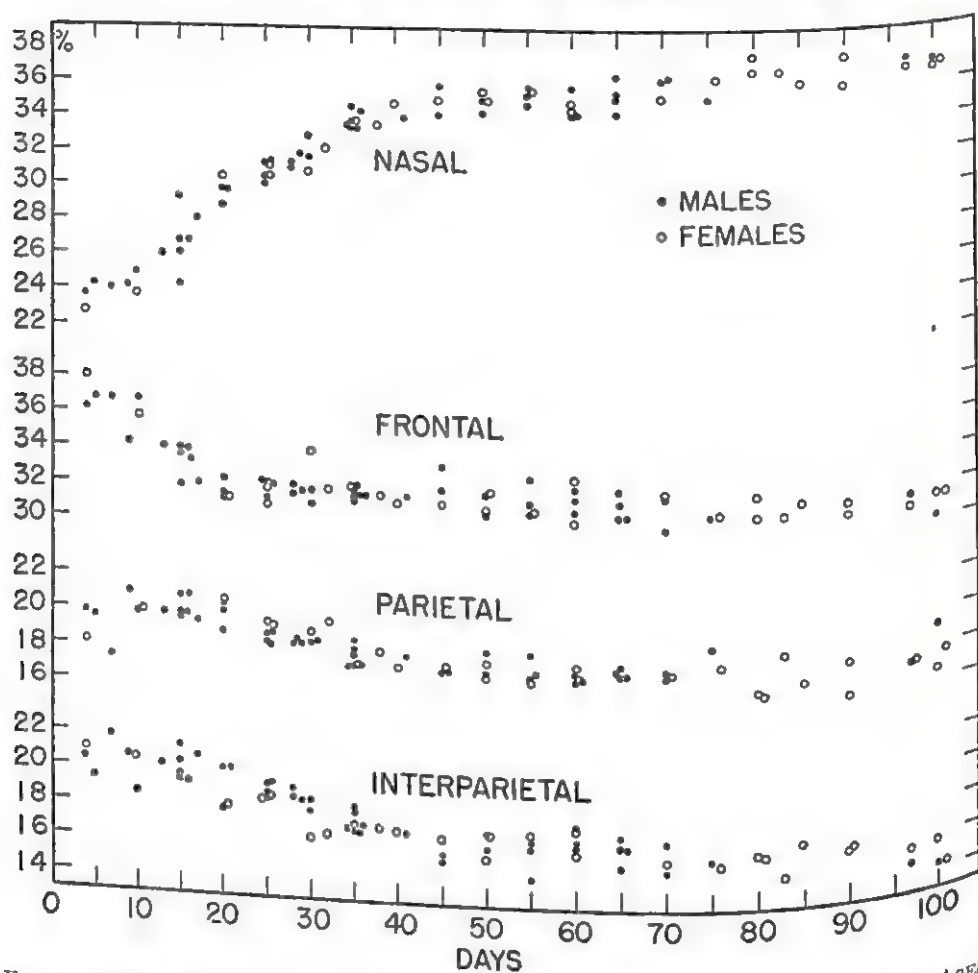


FIG. 7. PERCENTAGE OF TOTAL SKULL LENGTH OF INDIVIDUAL BONES AT DIFFERENT AGES.

The parietal and interparietal bones undergo continuous decrease in relative size through 100 days of age. The reduction in relative length of the frontals is less at successive ages, since growth at the frontonasal suture contributes greatly to the increased length of the face. The continuing relative decrease in total length of the frontals after 15 days of age is due in part to the early rapid deceleration of vault growth, and

in part to the great increase in the size of the nasal bones. The nasals are the only bones in the dorsal aspect of the skull showing increase in relative size after 15 days of age (table 5).

The postero-anterior gradient of dimensional increase in the dorsal aspect of the skull noted in the preceding section is reflected in proportional changes occurring from 15 through 100 days of age; the interparietal shows a relative decrease of 4.81%, the parietals of 2.73%, and the frontals of 2.41%; while the nasals increase 9.95% of total skull length.

*Changes in the Length-Breadth Proportions of the Skull.* The change in ratio of the length-breadth dimensions during the first 100 days of life contributes to the progressive dolichocephalization of the rat skull. The growth in biparietal width is completed by 35 days of age, while growth in length of the vault and face continues through 100 days of age. Continued growth of interparietal width after biparietal growth ceases results in a squaring off of the posterior end of the cranial vault. Biparietal width, which decreases 16.28% of total skull length, therefore undergoes a greater relative decrease in size than does interparietal width, which decreases only 10.97% of skull length from 5 to 100 days of age. Table 6 shows the relative size of the two breadth dimensions at different ages.

TABLE 6

*Relative width of the skull  
(percentage of total skull length)*

DAYS	BIPARIETAL WIDTH	INTERPARIETAL WIDTH
5	53.33	38.71
10	53.88	37.92
15	51.74	37.87
30	44.59	32.90
50	41.42	30.10
70	38.80	28.55
100	37.05	27.74

As in the case of cranial length, the greatest relative size of the cranial breadth occurs during the first 15 days of life. The fact that the width dimensions show little relative decrease in size from 5-15 days is due to the rapid lateral expansion of the brain case.

Comparison of the absolute and relative sizes of the individual bones at different ages (fig. 8) reveals the proportional changes occurring in the dorsal aspect of the skull.

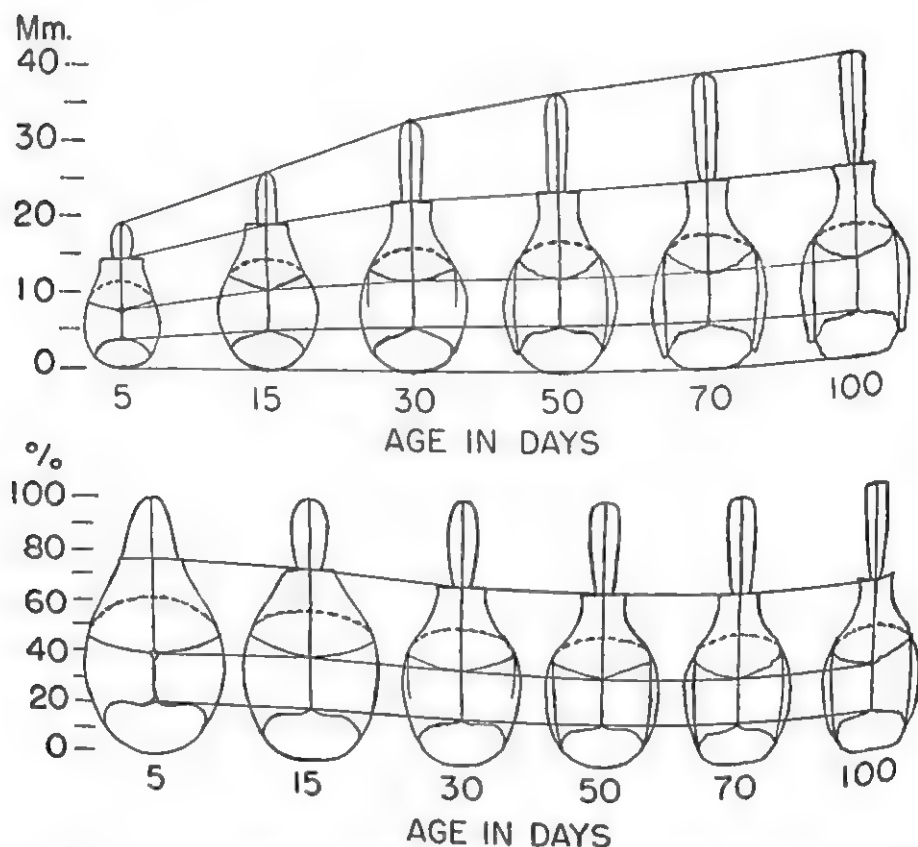


FIG. 8. ABOVE, GROWTH IN SIZE OF DORSAL ASPECT OF SKULL OF THE RAT. BELOW, PROPORTIONAL CHANGES IN DORSAL ASPECT OF SKULL OF THE RAT. ALL SKULLS DRAWN TO SAME TOTAL LENGTH TO SHOW DECREASE IN RELATIVE SIZE OF CRANIAL VAULT.

#### *Growth of the Cranial Base and Its Relation to the Form of the Skull*

We shall now consider the growth of the cranial base in conjunction with the growth of vault and face and the effect of the differential growth of these morphological units on the form of the skull.

*Patterns of Dimensional Increase of Vault Length, Face Length, and Base Length.* This analysis of dimensional changes is based on measurements taken in the midsagittal plane of the sectioned specimens, as follows:



*Base length*: total length of the basioccipital, basisphenoid, and presphenoid bones.

*Vault length*: total length from the posterior margin of the interparietal bone to the posterior border of the frontal sinuses.

*Face length*: total length from the posterior border of the frontal sinuses to the anterior margin of the nasal bones.

The dimensional increases of the base, vault, and face during the first 100 days of life result in a reversal of the size order found at 5 days of age: the vault is the longest of the three segments at 5 days and the shortest at 97 days of age, while the reverse is true of face length (table 7). Accordingly, if vault length is used as the standard of comparison, face length increases from 62.68% at 5 days to 119.83% of vault length at 97 days, while base length increases from 78.93% to 106.39% of vault length in the same period (table 7). The percentage values for base length show a slight decrease through 16 days of age, while face length maintains a consistent percentage increase throughout.

TABLE 7

*A. Dimensional increase of base, vault, and face (mm)*

DAYS	BASE LENGTH	VAULT LENGTH	FACE LENGTH
5	8.84	11.20	7.02
10	9.72	12.34	8.22
16	11.58	14.78	10.54
20	14.22	16.32	14.06
50	17.94	17.56	19.84
97	19.64	18.46	22.12

*B. Relative size of base and face (percentage of vault length)*

DAYS	BASE LENGTH/VAULT LENGTH	FACE LENGTH/VAULT LENGTH
5		62.68
10	78.93	69.01
16	78.77	71.31
20	78.35	89.83
50	87.13	112.98
97	102.16	119.83
	106.39	

Though the percentage ratios tend to emphasize the difference in relative magnitude of growth in these dimensions, a comparison of the incremental growth curves reveals that face length and base length follow a similar pattern of dimensional increase at variance with that indicated for the length of the vault (fig. 9). In terms of age intervals.

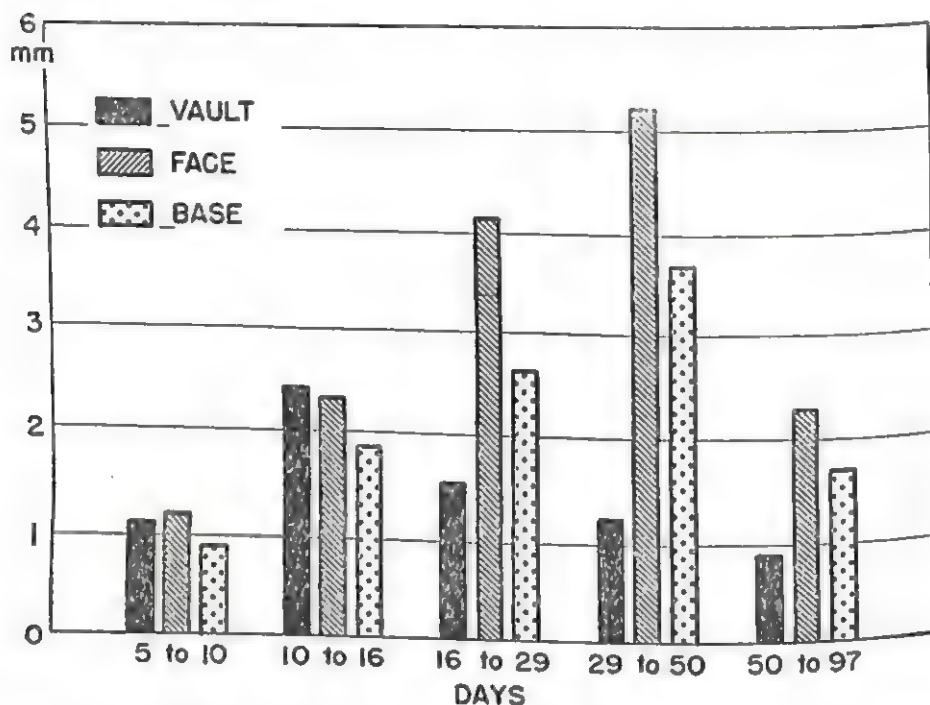


FIG. 9. INCREMENTAL GROWTH OF FACE, BASE, AND VAULT IN SKULL OF THE RAT.

both face and base show the greatest increase in length from 29 to 50 days of age, whereas the largest incremental increase of vault length occurs from 10 to 16 days of age. (This statement does not mean that the rate of growth of each of the segments is most rapid during the periods representing greatest dimensional increase, since the age intervals are obviously unequal.) Although face length grows more than base length at every age interval, the form of the incremental curves for these dimensions is nearly identical. The fact that the incremental increase in vault length occurring from 10 to 16 days of age is appreciably greater than that of the base during the corresponding period is responsible for the percentage decrease in base length.

Comparison of the ratios of the relative growth rates of the several dimensions further demonstrates a relationship between the patterns of growth for the face and base as contrasted with the vault. When the measurements of vault length are plotted against those of either face length or base length, on double-logarithmic paper, a curvilinear relationship is found, indicating change in the ratios of the relative rates of growth. However, when face length is plotted against base length the resulting curve approximates a straight line, showing that the ratio of the relative growth rates for these dimensions approaches a constant (fig. 10). The slope of the line indicates that face length has a greater rate of relative growth.

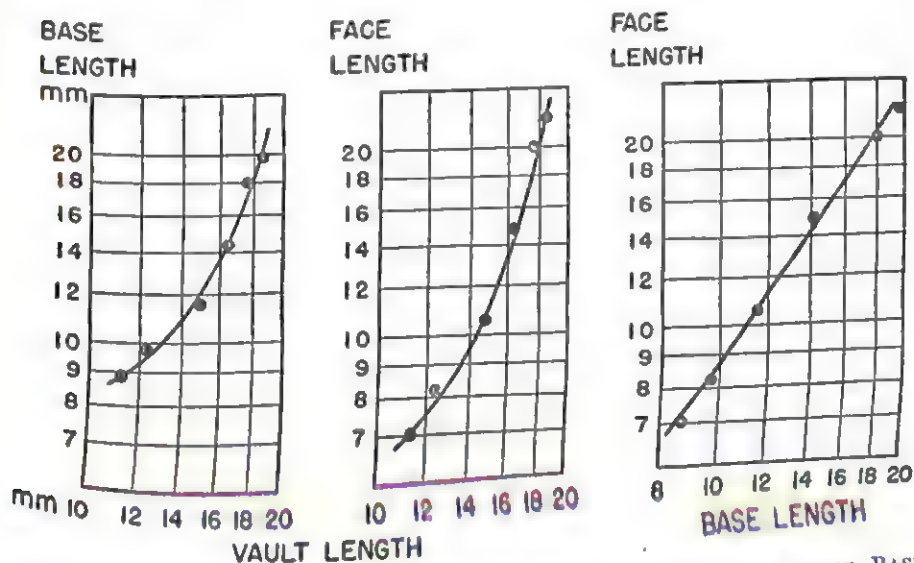


FIG. 10. DOUBLE-LOGARITHMIC PLOTTING OF VAULT LENGTH AGAINST BASE LENGTH AND FACE LENGTH, SHOWING CURVILINEAR FORM OF RATIOS OF RELATIVE GROWTH RATES CONTRASTED WITH LINEAR FORM OF RATIO OF BASE LENGTH WITH RESPECT TO FACE LENGTH.

*Developmental Changes in the Proportions and Form of the Skull.* The influence of differential growth on the proportions and form of the skull is here illustrated through a comparison of midsagittal sections made at different ages. Since increase in absolute dimension is not the immediate consideration, size differences have been eliminated by holding one morphological length constant in each series of diagrams in figure 11. This procedure also facilitates the analysis of the specific effect of differential growth in each of the morphological lengths. Base length is drawn to equal size in figure 11-A, while the same sections are represented with equal vault length in figure 11-B.

Since even adjoining bones show a changing spatial relationship during growth, a single bone, the basisphenoid, has been selected as

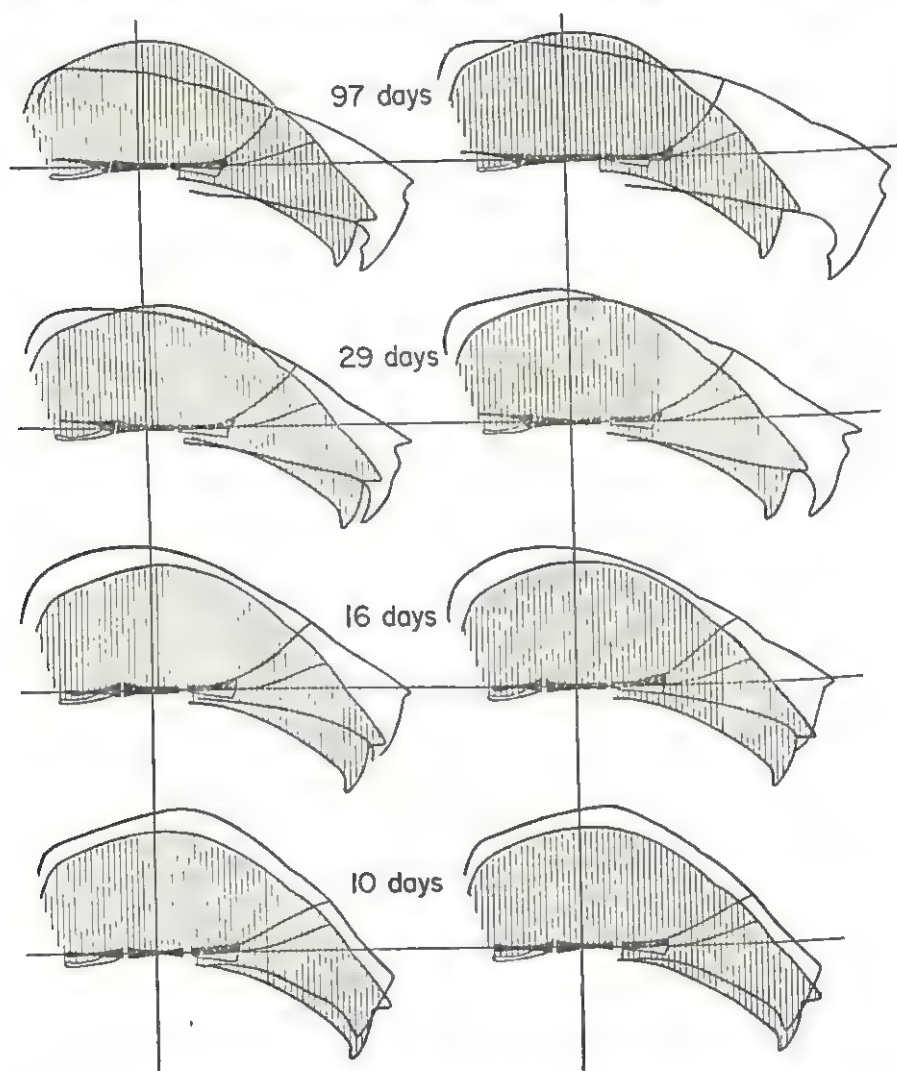


FIG. 11. MIDSAGITTAL SECTIONS OF SKULL OF THE RAT AT DIFFERENT AGES SUPERIMPOSED ON THAT OF A 5-DAY-OLD RAT: A. LEFT, BASE LENGTHS DRAWN TO SAME SIZE; B. RIGHT, VAULT LENGTHS DRAWN TO SAME SIZE. SKULLS ARE SUPERIMPOSED ON CENTER OF GROWTH IN LENGTH OF BASISPHENOIDS AND ORIENTED ON LONGITUDINAL AXIS OF THE SAME BONE.

determining the point and plane of superposition and orientation. The skulls are oriented on the long axis of the basisphenoid and superimposed on the center of growth in length of that bone.



*Changes in proportion.*

*The cranial vault.* If base length is held constant (fig. 11-A), the cranial vault exhibits a marked increase in relative height until approximately 15-20 days of age. During this time the relative length of the vault remains essentially unchanged. After 20 days of age the vault shows a progressive decrease in both relative height and relative length through 100 days of age. The decrease in relative height of the vault after approximately 15-20 days of age is also evident when vault length is held constant (fig. 11-B).

*The face.* If base length is held constant, the face shows a small increase in relative length from 10 to 16 days of age and very small relative increases thereafter (fig. 11-A). If vault length is held constant, however, the face undergoes considerable increase in relative length, particularly from 20 through 50 days of age (fig. 11-B).

*The base.* With the vault length held constant, the relative length of the base shows a slight decrease until 20 days of age and then increases continuously through 100 days of age.

*Changes in the form of the skull.* As a result of the differential growth of the individual bones the cranial form is modified concurrently with the observed changes in proportion. Analysis of the transformations at different ages in the rat skull indicates close dependence of form on the specific sites, timing, and direction of growth.

At 5 days of age the entire skull approximates the form of an arch: vault, base, and palate are dorsally convex, face and occiput are bent downward, and the cribiform plate of the ethmoid is deflected forward in nearly the same plane as the base.

From 5 to 10 days of age the rapid growth of the vault results in an even greater dorsal curvature in the region of the frontoparietal suture. Concurrently the slowly growing base unbends so that the three bones of which it is composed become aligned in the same plane. The rapid increase in height of the skull is accompanied by an upward, vertical shift of the cranial vault and face, relative to the base, with little change in the angulation of face, palate, or occiput.

From 10 to 16 days of age the greatest convexity of the vault is shifted posteriorly to the region of the parieto-interparietal suture. Owing to incremental growth at the maxillary tubercles, the alveolar arches become elongated and move forward from the cranial base, thereby providing space for the erupting molars. While the palate is moved forward in conjunction with the growth of the alveolar arches and aligned more closely in the plane of the base, growth at the maxillo-premaxillary sutures raises the anterior end of the face and decreases the dorsal curvature of the palate. Growth of the presphenoid anteriorly contributes to the forward movement of the cribiform plate of the ethmoid at the ventral margin. As a result of these changes the face is rotated forward and upward into a position anterior to the brain case.

After the major expansion of the cranial vault during the first 20 days of life, the more sustained growth of the bones comprising the base and the face results in a progressive modification of the skull toward a low, flat-vaulted dolichocephalic form.

In the base continued growth at the spheno-occipital synchondrosis results in the unbending of the occiput, elevation of the interparietal, and consequent reduction in curvature of the vault. The important factor in this modification is the greater increase in length of the posterior part of the base (basioccipital) as compared to the posterior portion of the vault (interparietal). The backward movement of the basioccipital swings the exoccipitals and the supraoccipital out from the base. Since the interparietal must be maintained in articulation with the supraoccipital, the interparietal is elevated at the posterior margin until it forms nearly a right angle with the posterior wall of the vault. The fact that the basioccipital element is also elevated with the occiput is evident in a comparison of midsagittal sections (fig. 11). These changes transform the base from a dorsally convex structure at 5 days of age to one slightly convex ventrally at 100 days of age.

The changing base-face relationship described earlier is continued through 100 days of age. The anterior end of the base is projected forward faster than the vault, owing to the greater addition of bone at both ends of the presphenoid than at the frontoparietal suture. The rotation of the ventral margin of the cribiform plate of the ethmoid toward an increasingly vertical position takes place in conjunction with the elongation of the base.

Since the frontomaxillary suture is curved backward and downward, growth at the upper, more vertical, part projects the face forward, while growth at the lower, more horizontal part moves the alveolar arches downward and forward. Growth at the sphenoid buttresses of the maxillary tubercles after the eruption of the molars deflects the posterior part of the dental arch ventrally. The combined effect, therefore, is one of continued rotation and elevation of the face into a plane more closely approximating that of the vault.

#### DISCUSSION

The data reported in preceding sections are here discussed in terms of their relevance for: (1) the nature of the growth processes and their methodological implications for the analysis of cranial form and (2) the significance of growth patterns for the interpretation of the factors influencing the form of the mammalian skull.

*Processes of Growth in the Skull.* To assess the changing form and proportions of the skull during ontogenetic development, attention must be directed toward determining the units of growth and the sites of bone deposition, rather than toward the histological nature of bone growth per se. In this connection, the proper selection of measurements depends on whether the skull grows essentially as a single unit, owing

to surface apposition and resorption, as claimed by Brash ('34), or whether increase in the size of the skull is the result of separating growth by incremental addition at the margins of the individual bones, as concluded by Massler and Schour ('51).

The findings here reported, derived from application of the vital-staining technique, indicate that both processes are operative in effecting an increase in the size of the rat skull, although they are of greatly unequal significance. Thus the individual bones (or the individual elements of a bone complex such as the occipital) comprise the units of incremental growth in the cranial vault, the cranial base, and the face, while the growth of the zygomatic arch, as a unit, results from the continuous surface apposition on the lateral aspect and surface resorption from the medial aspect. The arch of the rat is thus continuously reconstituted of new bony material during the course of lateral growth, in a manner very similar to the pattern of growth described by Brash for the zygomatic arch of the pig. Even in the rat, however, growth in length of the zygomatic arch takes place by incremental addition at the sutures.

The fact that independent investigations using the vital-staining technique can result in conflicting interpretations of the nature of growth processes in the skull requires explanation, however, if the derived data are assumed to have universal application for the interpretation of the mammalian skull. As far as the basic mechanisms of growth are concerned it matters little that different mammalian species were studied, but it is important to note that the youngest animal illustrated in Brash's paper is over 24 weeks of age, while the earliest age when madder-feeding ceased was 20 weeks. Brash does not indicate the ages at which madder-feeding was begun. Thus it is possible that the intersutural growth in the brain case of the pig (in conjunction with the rapid pattern of expansion of the brain) was completed before madder-feeding was begun. The early completion of intersutural growth observed in the cranium of the rat points to the necessity of beginning staining of specimens soon after birth and, further, of studying comparable phases of growth in different species.

While the role of the individual bone as a unit of accretionary growth in brain case and face is clearly evident, it must be recognized that variation in the number of sites of incremental bone deposition and in the amount of surface apposition will occur according to the particular architectural relationships existing in the skulls of different

species. For example, in the rat the incisors extend along the entire ventral aspect of the body of the mandible; therefore surface appositional growth of the alveolar bone at this site contributes considerably to the height of the mandibular body.

In the pig, however, the less specialized dentition is confined to the superior aspect of the body of the mandible, and Brash ('34) reports that the ventral aspect of the body does not comprise a site of bone growth contributing to an increase in the height of this structure. Aside from these differences, which are directly related to the specialized nature of the rat dentition, the mandible in both animals shows essentially the same sites and modes of growth. The relative massiveness of the skull in the species selected for study must also be considered. Thus the thin-boned cranium of the rat will demonstrate little surface apposition, while the heavy, thick bones of the pig cranium are the result of extensive surface apposition.

By measuring the total increment of bone deposited at each suture, Massler and Schour ('51) clearly demonstrated that proportional changes in the vault are due to unequal growth at the different sutures. The data here reported, however, indicate that the size of the increment contributed by each of the adjoining bones at a common suture is not always the same. In the case of the parieto-interparietal suture, particularly, the increment at the posterior margin of the parietal bones is roughly twice as large as that at the anterior margin of the interparietal bone.

The interpretation of Massler and Schour ('51) is that the intersutural trabecular growth is a response to tension caused by the intracranial pressure exerted by the expanding brain. However, the fact that differential growth takes place at a common tension line (suture) suggests that intracranial pressure is not the only factor controlling the growth of the bones in the cranial vault. It is possible that the centers of ossification have an individual specificity in terms of growth potential. This point has implications for the measurement of differential growth in the skull, since a single measurement of the total increment at a given suture may confound two different rates of bone deposition.

Thus far interpretation of the processes of growth revealed by the vital-staining technique has centered on the mechanisms by which increased size and proportional changes in the skull take place. A related problem concerns the mechanisms responsible for the changes in cranial *form* occurring concurrent to changes in proportion. Several



authors, as cited by Murray ('36), advance the hypothesis that as the radius of the cranium is increased the curvature of the individual bones must be reduced. Weinmann and Sieher ('47) and Brash ('34) contend that the flattening of the arc of each bone is accomplished by a process of differential apposition and resorption on the outer and inner surfaces of the vault, while Mair ('26) is of the opinion that only differential apposition occurs on both surfaces.

Neither of these interpretations is corroborated by the pattern of bone deposition observed during the extensive longitudinal flattening of the rat vault. No evidence was found of resorption from the surfaces of the vault or differential apposition sufficient to account for the radical changes in relationship of the vault bones during the first 100 days of life. To postulate that the mechanism responsible for the extreme flattening of the rat vault comprises a surface phenomenon, one must assume complete reconstitution of the component bones by successive replacement of the bony material.

An alternative hypothesis is offered here: that the changes in form of the rat skull are the result of spatial reorientation of the individual bones, and that the differential growth of the inner and outer cortical plates observed at the sutural margins represents the mechanism of adjusting the changing relationship of adjoining bones. The relative significance of unequal growth of the cortical plates in modifying cranial form could be tested by microscopic measurement of sections through the sutures of stained specimens of different species.

The evidence indicating the sites of cranial growth, as revealed through experimental investigation, greatly simplifies the problem posed by Reeve and Huxley ('46) concerning the unit of growth regarded as a basis for exploring allometric relationships or differential growth in general. For the analysis of relative growth as a mechanism of evolutionary change (Simpson, '44), particularly in the case of paleontological materials, where determination of growth increments is impossible, the diameters of individual bones in the skulls of related groups may be measured. In the case of laboratory animals, however, determination of the increment of growth at specific sites and at particular time periods, made possible by the vital-staining technique, permits the study of differential growth rates within a single bone. Further, this approach opens an avenue for the study of the related problem of the existence of gradients of growth in such structures as the cranium and the face, as suggested by the work of Thompson ('17) and discussed by Huxley ('32) and Child ('41).

In selecting points or planes for superpositioning serial tracings of skulls, prior analysis by the vital-staining technique indicates the sites of active bone deposition responsible for directional growth in the skull. Selection of points for superpositioning therefore need not be based on conventional landmarks assumed to maintain a stable position in the skull. Rather, the investigator can take account of the directions of growth and changing spatial relationships of the bones in the particular species under consideration. In this connection it is important to recognize that an anatomic landmark that shows no evidence of bone deposition cannot for that reason be assumed to be a fixed point in the skull.

For example, the point basion in the rat is shifted posteriorly, owing to addition of bone at the spheno-occipital synchondrosis, while there is no evidence of addition of bone at this point proper. In the rat, moreover, the conformation of the cranial vault undergoes considerable modification after growth in this region is essentially completed, owing to accommodation of the bones in the vault to continued growth of the base.

These facts illustrate the complexity of selecting points in the skull as a basis for establishing a plane assumed to have interspecific validity. Since the complex changing spatial relationships of the bones in the skull are a function of different rates of growth at all sites contributing to incremental growth, selection of a basis for superpositioning ultimately leads to the conclusion that successive growth changes can be viewed only in reference to a single bone in the skull. As Krogman ('51, p. 414) remarks, "there are, as far as we know, no two points in head and/or face which, during growth, stand in unvarying relation to one another."

*Patterns of Growth and Change in Form of the Skull.* The growth pattern of the rat skull is the result of two basic systems of growth: (1) early rapid expansion of the brain case in conjunction with the growth of the brain and (2) slower growth of longer duration, resulting in elongation of the cranial base and forward projection of the face. These systems are evidenced by the growth curves of the individual bones comprising the vault and the base-face complex and by the duration of active bone deposition at specific growth sites, as revealed by alizarin staining.

The changing form described for the rat skull is a function of the sequential influence of these primary systems of growth. During the first 20 days of life rapid growth of the brain is the major factor

determining cranial form. After the early expansion of the brain case, however, the more persistent growth of base and face result in an unbending of the skull from the cranial base, correlated flattening and reduction in the relative height of the vault, posterior movement of the foramen magnum, and elevation of the occiput posteriorly and the face anteriorly. These changes in form are directly attributable to the altered spatial relationships between the bones in the vault and those in the base-face complex. This altered relationship is brought about by the disproportionately greater growth of the base-face complex subsequent to enlargement of the brain.

Reference to the literature on the development of the anthropoid skull and the human skull shows that the systems of growth and their influence on the form of the skull, as described here, are not only characteristic of the rat but also represent deep-seated factors affecting the form of the mammalian skull. Thus Schultz ('40, '41), in detailing ontogenetic changes in the skulls of the chimpanzee and the orangutan, emphasizes: the extremely rapid growth of the brain during the infantile period (to 85 and 90% of adult size for chimpanzee and orangutan, respectively); the subsequent enormous expansion of the face in conjunction with eruption of the permanent dentition and therewith the backward shift in position of the occipital condyles and the foramen magnum; and migration of the orbits from beneath the brain to a position almost in front of it.

The changes in cranial form resulting from the early completion of cranial growth and the more sustained expansion of the face are clearly revealed in Schultz's illustrations (fig. 12). Since Schultz conveniently reduced the skulls at all ages to the same length, the striking backward migration of basion clearly demonstrates the disproportionately greater increase in length of the cranial base over the length of the cranial vault. Of particular significance for the present discussion is the fact that, with the greater elongation of the base, the occipital squama is reoriented nearly into the vertical plane, while the orbits are elevated to a position in front of the brain. These changes are instrumental in producing the progressive flattening of the cranial vault and the radical modification in cranial form in the chimpanzee and the orangutan after the growth of the brain in these animals is essentially completed.

Similarly, the development of the gorilla skull shows the effect of basilar growth on cranial form. Krogman ('31, p. 106), in discussing the changing dimensions of the posterior aspect of the skull, comments:

"The increase noted is the measure of the backward and upward swing of the foramen magnum. . . . Here the period just preceding and succeeding the eruption of the first molar is the time of greatest movement, and again just before the eruption of the third molar, at a time when the superior portion of the occiput of the male skull is being sharply pulled forward and up, shifting the inferior portion backward and up."

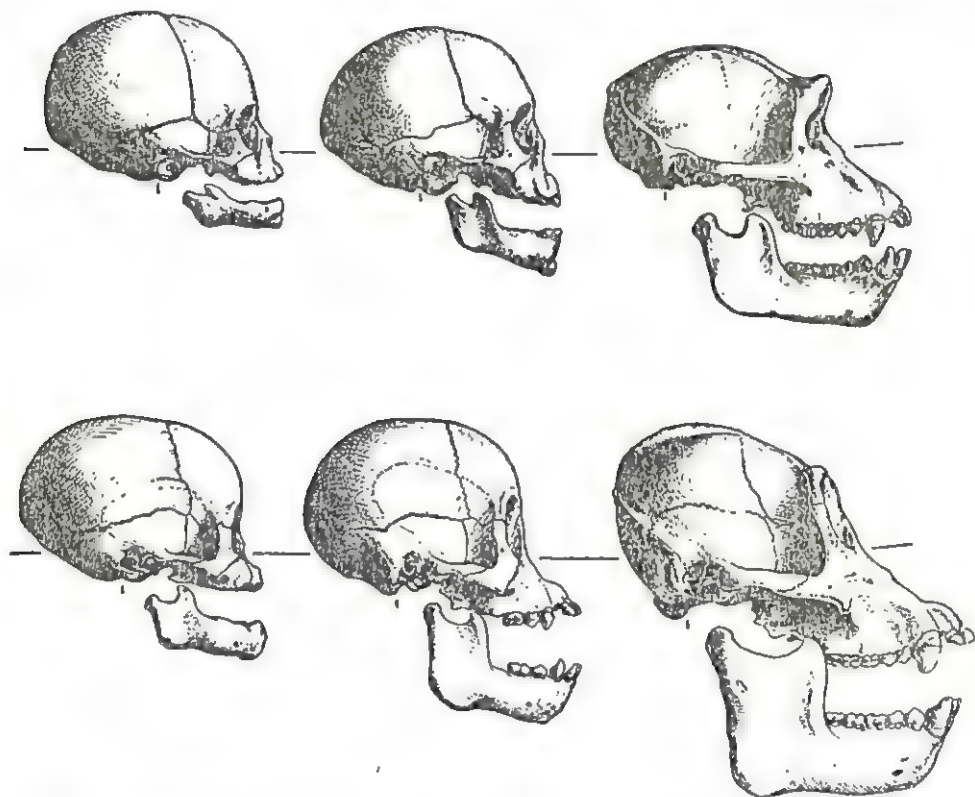


FIG. 12. TOP, LATERAL VIEW OF FEMALE FETAL, INFANTILE, AND ADULT CHIMPANZEE SKULLS DRAWN TO SAME SKULL LENGTH. (AFTER SCHULTZ, '40.) BOTTOM, LATERAL VIEW OF MALE NEWBORN, INFANTILE, AND ADULT ORANGUTAN SKULLS DRAWN TO SAME SKULL LENGTH. (AFTER SCHULTZ, '41.) IN EACH CASE BASION IS INDICATED BY VERTICAL LINE.

These modifications take place, it should be noted, after the period of rapid cranial growth, during which the brain was the chief determinant of cranial form.

The form of the human skull, in contrast to that of the anthropoid, appears to undergo relatively little change during ontogenetic develop-



ment. On the basis of a serial roentgenological study of the same individuals from three months to 8 years of age, Brodie ('41, p. 251) concluded that "the morphogenetic pattern of the head is established by the third month of postnatal life, or perhaps earlier, and that once attained it does not change."

Brodie's conclusions reinforce the findings of such comparative anatomists as Welcker, Bolk, Schultz, Weidenreich, Krogman, and others concerning the relative stability, in the modern human skull, of the position of such structures as the foramen magnum, the orbits, and the cranial base, and of the general configuration of the cranium. Thus it is evident that a much closer correspondence exists in the growth rates of the component structures of the skull in man than is to be found in those of anthropoids.

However, certain facts suggest that modern man reflects the same pattern of early cranial expansion and subsequent more sustained growth of the cranial base as that found in the anthropoids, although in lesser degree. Thus Scammon ('30) indicates that by 8 years of age (the age at which Brodie's study was terminated) the brain has completed 95% of its total growth, and the data of Simmons ('44) show that approximately 94% of adult head length and breadth have been attained at this age. Count's ('42) analysis of Brodie's data on the cranial base indicates that at 8 years of age the length of the base from sella turcica posteriorly has a higher rate of growth than the anterior cranial floor from sella turcica to nasion; and further, that the rate of growth of the anterior length decelerates more rapidly.

Probably related to the more sustained growth of the posterior part of the base is the fact that the cartilaginous plate at the spheno-occipital synchondrosis is not completely replaced by bone until approximately the 18th year of life (Weinmann and Sicher, '47).

These facts are highly suggestive of the influence of differential growth in cranial vault and cranial base in bringing about the slight elongation of the head observed during growth. They warrant further study of ontogenetic changes in form after cessation of brain growth.

The interpretation here advanced is in conflict with Weidenreich's ('41) theory, namely, that the brain is the sole determinant of form in the mammalian skull and that the enlargement of the brain has a depressing influence on the growth of the face. However, a consideration of the changes in form, both ontogenetic and phylogenetic, detailed by Weidenreich for various mammalian groups shows no essential incompatibility with our interpretation.

Further, the data on microcephalic subjects discussed by Weidenreich himself furnish evidence of the importance of the growth of base and face in determining cranial form. Weidenreich illustrates the skull and endocast of a Basuto microcephal (his figures 40 and 43) and describes the "anthropoid characteristics" of the skull. He remarks (p. 396) that "the form and proportions of the brain . . . fail to show any appreciable differences when compared with the normal human brain." The form of this skull and microcephalic skulls in general he attributes to the fact that the brain grew to only a small size. Such an explanation accounts only for the absolutely small size of the vault. The ultimate form of the microcephalic skull is due rather to continued growth of face and base to nearly normal size after the arrest of brain growth. The accommodation of arrested vault growth to the continued growth of the base is reflected in Weidenreich's ('41, pp. 393, 394) comment concerning one of the skulls he describes, that "it is of great interest that there is no indication of a deflection of the cranial base as is characteristic of man but that its axis forms a perfectly straight line as in gorilla." (See his figures 29 and 42.)

The more extreme condition in which the brain is absent (anencephaly) further illustrates the independence of the base-face complex during development. De Beer ('37, p. 485) states: "In such skulls there is no cranial vault at all, and the bones which would normally form it are present but extremely small and abnormal. On the other hand, the bones of the skull-base (basioccipital, basisphenoid, petriotic, etc.) are fairly normal, as are those of the face."

Conversely, the data drawn from other types of pathological conditions, such as achondroplasia, in which the growth of the base is arrested, present a situation where the expansion of the brain constitutes the sole determinant of the form of the skull. In such instances the failure of the base-face complex to elongate leaves the skull in a globular form, with a highly arched base and a depressed nasal region. It is significant that in describing the alterations required to correct the deficiencies in the form of the achondroplastic skull, Stockard ('41) details a series of changes in exact reverse to those postulated by Weidenreich as having occurred in human phylogeny.

Turning more directly to the problem of interpreting the evolutionary changes in human cranial form, it would appear that the progressive brachycephalization of the hominid skull cannot be regarded simply as a function of an allometric growth relationship, in which

the brain is the independent variable and the face the dependent variable. Such an interpretation reduces the form of the skull to a single system of growth in which the face has no adaptive significance.

The data presented here suggest, rather, that the form of the skull is primarily the result of the interaction of two functional systems of growth. If an allometric relationship is present in the skull it would appear to relate the base to the face, rather than the brain case to the face. In terms of the causal determinants of cranial form, the brachycephalization of the human skull would appear to be the product of an adaptive trend in which the size of the brain and the size of the face have differential selective value.

#### SUMMARY

The purpose of this study was to determine the processes and systems of growth influencing the form of the mammalian skull. The experimental technique of staining the growing bone in the rat with alizarin red S was used in order: (1) to reveal the specific sites and modes of growth resulting in an increase in the size of the skull and (2) to assess the effects of differential growth at these sites in modifying cranial form.

The following findings are reported:

1. Increase in the size of the skull takes place as the result of two growth processes. The enlargement of the brain case and the face is due to separating growth at the sutures and at the synchondroses by incremental addition at the margins of each center of ossification. The zygomatic arch grows as a single unit by continuous surface apposition on the lateral aspect and surface resorption from the medial aspect. The individual bone, therefore, comprises the unit of growth in the brain case and the face.

2. Proportional changes in the brain case and the face are effected by differential growth at the sutures and at the synchondroses joining the individual bones. Differential growth thus results in changes in the diameters within the individual bones and also in unequal size increase between the component bones of the brain case and the face.

3. Modifications in the cranial form of the rat are caused by spatial reorientation and changing accommodation among individual bones necessitated by disproportionate growth. Differential growth of the inner and outer cortical plates at the sutural margins is the mechanism of adjusting the changing relationship of adjacent bones. No evidence

was observed of resorption from the surface of the cranial vault or differential apposition sufficient to account for the radical changes in relationship of the vault bones during the first 100 days of life.

4. The growth pattern of the rat skull is the result of two basic systems of growth: (a) early rapid expansion of the brain case in conjunction with the growth of the brain and (b) slow growth of longer duration, resulting in elongation of the cranial base and the face. These systems are evidenced by the growth curves of the individual bones comprising the cranial vault and the base-face complex and by the duration of active bone deposition at specific growth sites, as revealed by alizarin staining. The changing form described for the rat skull is a function of the sequential influence of these primary systems of growth.

5. Reference to the literature on the ontogenetic development of anthropoid and human skulls shows that the systems of growth described for the rat represent deep-seated factors affecting cranial form. Examination of ontogenetic changes in the form of the skull of the chimpanzee, the orangutan, and the gorilla reveals a pattern of early, rapid cranial expansion, followed by more sustained growth of the cranial base and the face. The interaction of these two systems of growth results in flattening and progressive elongation of the cranium of the anthropoid, accompanied by backward migration of the foramen magnum and elevation of the occiput. Related data on human microcephalic, anancephalic, and achondroplastic subjects further substantiate the existence of two basic systems of growth and the influence of growth failure on the part of either system on cranial form.

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## LITERATURE CITED

- BRASH, J. C. 1934 Some problems in the growth and developmental mechanics of bone. *Edinburgh Med. J.*, n.s. 4th, 41: 305-387.
- BRODIE, A. G. 1941 On the growth pattern of the human head. *Am. J. Anat.*, 68: 209-262.
- CHILD, C. M. 1941 *Patterns and Problems of Development*. University of Chicago Press.
- COUNT, E. W. 1942 A quantitative analysis of growth in certain human skull dimensions. *Human Biol.*, 14: 143-165.
- DE BEER, G. R. 1937 *The Development of the Vertebrate Skull*. Oxford Press.
- HUNTER, JOHN 1771 *Natural History of the Human Teeth*. John Johnson, London.
- HUXLEY, J. S. 1932 *Problems of Relative Growth*. Methuen, London.
- KEITH, A. 1910 Description of a new craniometer and of certain age changes in the anthropoid skull. *J. Anat.*, 44: 251-270.
- KROGMAN, W. M. 1931 Studies in growth changes in the skull and face of anthropoids. Pt. III, Growth changes in the skull and face of the gorilla. *Am. J. Anat.*, 47: 89-115.
- 1951 Craniometry and cephalometry as research tools in growth of head and face. *Am. J. Orthodontics*, 37: 406-414.
- MAIR, R. 1926 Untersuchungen über die Struktur der Schädelknochen. *Ztschr. mikr.-anat. Forsch.*, 5: 625-666.
- MASSLER, M. 1941 The growth pattern of the cranial vault in the albino rat as measured by vital injections of alizarine red "S." Unpublished Master of Science thesis. University of Illinois, Chicago.
- and I. SCHOUR. 1951 The growth pattern of the cranial vault in the albino rat as measured by vital staining with alizarine red "S." *Anat. Rec.*, 110: 83-101.
- MOORE, A. W. 1940 Head growth of the macaque monkey as revealed by vital staining, embedding, and undecalcified sectioning. *Am. J. Orthodontics*, 35: 654-671.
- MURRAY, P. D. F. 1936 *Bones*. Cambridge University Press.
- REEVE, E. C. R. AND J. S. HUXLEY 1945 Some problems in the study of allometric growth. In W. E. L. CLARK AND P. B. MEDAWAR, *Essays on Growth and Form*. Oxford University Press.
- ROBB, R. C. 1935 A study of mutations in evolution. Pt. I, Evolution in the equine skull. *J. Genetics*, 31: 39-46.
- ROMER, A. S. 1948 Relative growth in pelycosaurian reptiles. In A. L. DU TOIT (ed.), *Robert Broom Commemorative Volume*. Royal Society of South Africa, Capetown.

- SCAMMON, R. E. 1930 The measurement of the body in childhood. In J. A. HARRIS AND OTHERS, *The Measurement of Man*. University of Minnesota Press, Minneapolis.
- SCHULTZ, A. H. 1940 Growth and development of the chimpanzee. *Carnegie Inst. Publ.* 518, *Contr. Embryology*, 170: 1-63.
- 1941 Growth and development of the orang-utan. *Carnegie Inst. Publ.* 525, *Contr. Embryology*, 182: 57-110.
- SIMMONS, KATHERINE 1944 Brush Foundation study of child growth and development. II, Physical growth and development. *Monogr. Soc. Res. Child Developm.*, 9, no. 1.
- SIMPSON, G. G. 1944 *Tempo and Mode in Evolution*. Columbia University Press, New York.
- SNEDECOR, G. W. 1946 *Statistical Methods*. Iowa State College Press, Ames, Iowa.
- STOCKARD, C. R. 1941 *The Genetic and Endocrine Basis for Differences in Form and Behavior*. Wistar Institute, Philadelphia.
- THOMPSON, D'A. W. 1917 *On Growth and Form*. Cambridge University Press.
- WADDINGTON, C. H. 1950 The biological foundations of measurements of growth and form. In S. ZUCKERMAN AND OTHERS, *A discussion on the measurement of growth and form*. *Proc. Roy. Soc., London, B.*, 137: 433-523.
- WASHBURN, S. L. 1947 The relation of the temporal muscle to the form of the skull. *Anat. Rec.*, 99: 239-248.
- 1953 The strategy of physical anthropology. In A. L. KROEBER AND OTHERS, *Anthropology Today*. University of Chicago Press.
- WEIDENREICH, F. 1941 The brain and its role in the phylogenetic transformation of the human skull. *Tr. Am. Philosoph. Soc., n. s.* 31: 321-442.
- 1945 The brachycephalization of recent mankind. *Southwestern J. Anthropol.*, 1: 1-54.
- WEINMANN, J. P. AND H. SICHER 1947 *Bone and Bones*. C. V. Mosby, St. Louis.
- YOUNG, J. Z. 1950 The exact description of living organization. In S. ZUCKERMAN AND OTHERS, *A discussion on the measurement of growth and form*. *Proc. Roy. Soc., London, B.*, 137: 433-523.





# ON THE RELATIONSHIP BETWEEN MENARCHEAL AGE AND ADULT BODY STRUCTURE

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## INTRODUCTION

WITH the advent of puberty the infantile body-build begins to change in a masculine or feminine direction. The nature of the resulting sex differences in adult body-build has been investigated somatometrically by Wollf and Steggerda ('43), Bayley and Bayer ('46), Reynolds ('49), Tanner ('51), Edwards ('51), Garn and Saalberg ('53), Lindegård ('53) and others. The adult female body-build differs from the male especially in the following respects. In females the long-bone lengths, the degree of skeletal sturdiness and the total amount of muscle tissue are smaller than in males, while the thickness of the subcutaneous fat layer is larger. In addition the sexes differ with respect to the proportions between certain body dimensions. In females the upper extremities are shorter in proportion to the lower. Further, females have a larger bi-iliac breadth in proportion to the bi-acromial breadth as well as to the lengths of the long bones.

The purpose of the present study was to ascertain to what extent any relationship exists between the age of menstrual onset and the adult female body structure.

## MATERIAL

The investigation was based on a material consisting of somatometric and functional data concerning 300 adult Norwegian hospital nurses. The material was collected and published by Schiøtz ('36). The same series was employed by Lindegård ('53) for an analysis of sex differences in body-build.

The ages of these women ranged from 20 to 34 years, the mean being 23.6 years. Sixty-nine per cent belonged to the age group 20-24 years; only 1.2% were more than 30 years old.

Data about the age at which menstruation initially occurred were available in 288 cases. Concerning the remaining 12 cases figures were

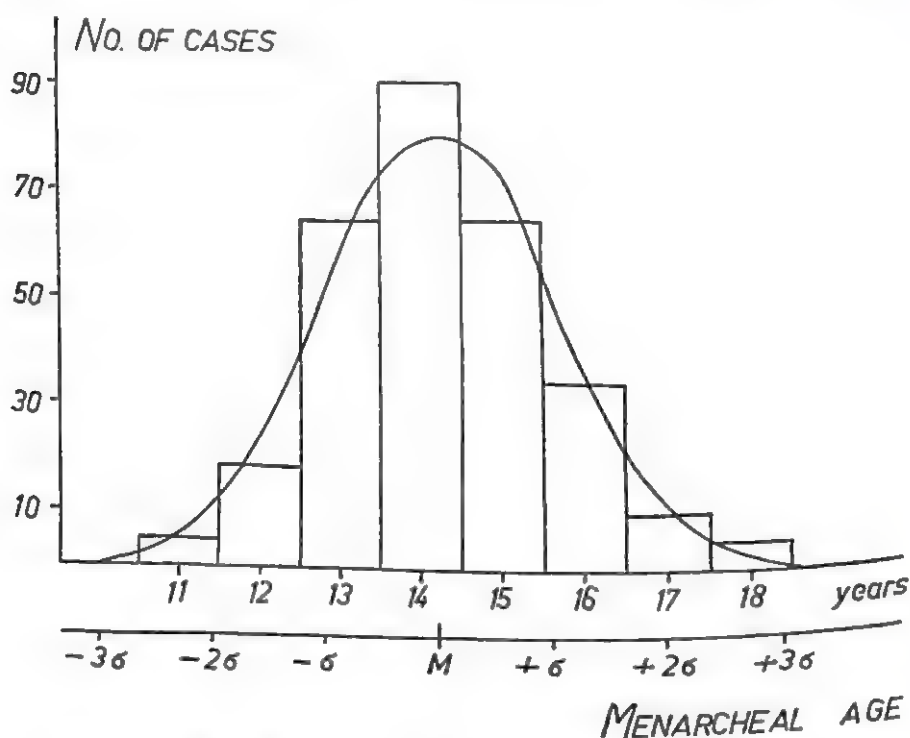


FIG. 1. COMPARISON BETWEEN THE FREQUENCY DISTRIBUTION OF THE MENARCHEAL AGE AND THE NORMAL DISTRIBUTION CURVE.

lacking or uncertain. The menarcheal ages ranged from 11 to 18 years, the mean being  $14.2 \pm 0.1$  years with a standard deviation of 1.4 years. The frequency distribution of the menarcheal age agrees visually well with the normal frequency distribution (figure 1).

#### METHODS

Body structure was analysed according to a method devised by Lindegård ('53). This method somatometrically rates the position of an individual on scales for certain continuous variables. The system comprises 4 variables, called *length*, *sturdiness*, *muscle* and *fat factors*,

referring to the amount and distribution of bone, muscle and fat tissues. A new method, devised by Lindegård ('53) for partial correlation and regression, was used to calculate the individual values of these and other measures of body structure. The calculations are illustrated by the following example.

In the present series the regression of the hand length on the radius length is satisfied by the linear function  $Y = 0.34X + 8.9$ , in which  $X$  denotes the radius length. From this regression the difference between the hand length and corresponding regression mean is determined. In this way the *residual* hand length after elimination of its interdependence with the radius length, i. e.  $F$  hand length (radius length), is obtained for each case. The residual expresses the divergence of hand length in an individual from the average hand length of persons with the same radius length. By determining the residuals for every case in the series a *residual distribution* is obtained. The residuals can be subjected to new correlation or regression analysis with regard to either absolute dimensions or other residuals (cf. fat factor below).

The following measurements or residuals represent the different factors:

*length factor*: radius and tibia lengths,

*sturdiness factor*: the residuals  $F$  hand length (radius length) and  $F$  foot length (tibia length),

*muscle factor*: strength of hand grip,

*fat factor*: the residual  $F$  body-weight (stature, muscle factor).

The series was arbitrarily divided into three groups according to menarcheal age. Below, these groups are called the "early group" (menarcheal age 11-13 years), the "median group" (menarcheal age 14 years) and the "late group" (menarcheal age 15-18 years).

In the analysis of the fat factor two cases (belonging to the early group) were excluded because of obesity. The fat factors of those cases were +18.8 kg. (equal to +3.6 standard deviation units) and +26.5 kg. (equal to +5.1 standard deviation units) respectively. These two cases were also excluded in the analysis of the relationship between the bi-iliac breadth and other dimensions.

In order to calculate the significance of a difference between arithmetical means, the difference was tested by the *t-test* (Snedecor, '46). A difference found was considered statistically significant (\*\*), if the probability of the difference being due to chance was less than 1%. If this probability was equal to, or greater than, 1%, but less than 5%, the difference was considered statistically probable (\*).



TABLE 1

*Different Body Measurements and Residual Expressions for Three Groups of Adult Females, Classified According to Menarcheal Age, and a Comparison Between the Body-Build and Early and Late Menarche*

MEASUREMENT OR RESIDUAL EXPRESSION	MENARCHEAL AGE 11-13 YEARS (87 cases)		MENARCHEAL AGE 14 YEARS (90 cases)		MENARCHEAL AGE 15-18 YEARS (111 cases)		DIFFERENCE $M_1 - M_3$
	$M_1 \pm \epsilon_{M_1}$	$\sigma_1$	$M_2 \pm \epsilon_{M_2}$	$\sigma_2$	$M_3 \pm \epsilon_{M_3}$	$\sigma_3$	
Length factor							
Tibia length in cm.	36.7 $\pm$ 0.3	2.3	37.1 $\pm$ 0.2	2.1	37.5 $\pm$ 0.2	2.3	0.8 $\pm$ 0.3 2.4*
Radius length in cm.	23.1 $\pm$ 0.1	1.2	23.1 $\pm$ 0.1	1.1	23.6 $\pm$ 0.1	1.1	0.5 $\pm$ 0.2 2.9**
Sturdiness factor							
Mean of $F$ hand length (radius length) and $F$ foot length (tibia length) in standard deviation units	0.0 $\pm$ 0.1	1.0	-0.1 $\pm$ 0.1	0.8	+0.1 $\pm$ 0.1	0.8	0.1 $\pm$ 0.1 1.2
Muscle factor							
Hand-grip strength in dynamometer units	34.5 $\pm$ 0.8	7.1	33.7 $\pm$ 0.7	7.0	34.4 $\pm$ 0.8	7.9	0.1 $\pm$ 1.0 0.1
Fat factor							
$F$ weight (stature, muscle factor) in kg.	+0.6 $\pm$ 0.6	5.2	-0.3 $\pm$ 0.5	5.0	-1.6 $\pm$ 0.5	5.6	2.2 $\pm$ 0.9 2.8**
Proportions							
$F$ radius length (tibia length) in cm.	-0.1 $\pm$ 0.1	1.0	-0.3 $\pm$ 0.1	1.0	+0.1 $\pm$ 0.1	0.8	0.2 $\pm$ 0.1 1.4
$F$ bi-iliac breadth (bi-acromial breadth) in cm.	0.0 $\pm$ 0.2	1.5	0.0 $\pm$ 0.1	1.2	+0.1 $\pm$ 0.1	1.2	0.1 $\pm$ 0.2 0.5
Other measurements							
$F$ bi-iliac breadth (radius length) in cm.	-0.1 $\pm$ 0.2	1.5	-0.1 $\pm$ 0.1	1.3	0.0 $\pm$ 0.1	1.2	0.1 $\pm$ 0.2 0.5
Stature in cm.	162.2 $\pm$ 0.6	5.8	162.3 $\pm$ 0.5	4.9	163.4 $\pm$ 0.4	4.5	1.2 $\pm$ 0.8 1.6
Body weight in kg.	61.1 $\pm$ 0.8	7.5	60.0 $\pm$ 0.7	6.3	59.8 $\pm$ 0.6	6.5	1.3 $\pm$ 1.0 1.3

$M$  = arithmetic mean,  $\epsilon_M$  = error of mean,  $\sigma$  = standard deviation,  $\epsilon_{diff.}$  = error of difference,  $t$  = quotient between the difference and its error. All calculations were made with two decimals, here reduced to one.

## RESULTS

The mean values of certain measurements and residual expressions were calculated for each one of the three menarcheal age groups. The result obtained are summarized in table 1.

## DISCUSSION

Significant differences in magnitude of length and fat factors were found between the early and late groups. In the early group the length factor was smaller, while the fat factor was larger.

The differences between early and late groups in sturdiness and muscle factors did not reach the level of statistical probability. However, it should be pointed out that the median group had a smaller sturdiness factor than did the late group. That difference was statistically probable ( $t = 2.0^*$ ), but the difference between the values of the sturdiness factor in the early and median groups was not ( $t = 0.5$ ).

The relation of menarcheal age to body configuration was studied by Barker and Stone ('36), the body-build then being registered typologically according to Kretschmer. The results obtained by these authors suggested a tendency of females with an early menstrual onset to develop towards the pyknic type, and of females with a late onset to develop towards the leptosomatic type. These assumptions are supported by the results obtained in the present investigation, as, according to Lindgård ('53), the pyknic type corresponds to an individual with small long-bone lengths and relatively large amount of body-fat, and the leptosomatic type to an individual with large lengths of the long bones and a relatively small amount of body-fat.

The results of the present investigation indicate that, concerning the length, fat, and sturdiness factors, women with a relatively early menstrual onset tend to develop a more pronounced "feminine" adult body structure than do women with a relatively late onset.

In view of these findings the menarcheal age groups were analysed in regard to body build proportions which vary with sex.

The proportion between the radius and tibia lengths did not show even a probable difference between the early and late groups. However, in the median group the radius length was smaller in proportion to the tibia length than in the late group. This difference was significant ( $t = 3.1^{**}$ ). The corresponding difference between the early and median groups was not even statistically probable ( $t = 1.3$ ).

Thus, an analysis of the proportion between the radius and tibia

lengths also suggested that women with an earlier menarcheal age will develop a more pronounced "feminine" adult body-build than do women with a later onset of menstruation.

The proportion between the bi-iliac breadth and the bi-acromial breadth is a marked sex-characteristic. Further, Lindegård ('53) showed that the bi-iliac breadth in proportion to the long-bone lengths is larger in females than in males. In the present investigation, however, no differences were noted between the menarcheal age groups concerning these proportions.

#### SUMMARY AND CONCLUSION

A series of 288 Norwegian adult women was studied for any relationship between the age of menstrual onset and adult body structure. The results obtained indicate a tendency of individuals with an early menarcheal age to develop a more pronounced "feminine" adult body structure than do individuals with a late début of menarche. The menarche being an estrogen mediated phenomenon it might also be concluded that individuals with an early onset of the pubertal estrogen increment tend to acquire a more "feminine" adult body build than do individuals in whom this onset is late.

#### ACKNOWLEDGMENT

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#### LITERATURE CITED

- BARKER, R. G. AND C. P. STONE 1936 Physical development in relation to menarcheal age in university women. *Human Biol.*, 8: 198-222.
- BAYLEY, N. AND L. M. BAYER 1946 The assessment of somatic androgyny. *Am. J. Phys. Anthropol.*, n. s. 4: 443-461.
- EDWARDS, D. A. W. 1951 Differences in the distribution of subcutaneous fat with sex and maturity. *Clin. Sc.*, 10: 305-315.
- GARN, S. M. AND J. H. SAALBERG 1953 Sex and age differences in the composition of the adult leg. *Human Biol.*, 25: 144-153.
- LINDEGÅRD, B. 1953 Variations in human body-build. *Acta psychiat. et neurol.*, Suppl. 86.
- REYNOLDS, E. L. 1949 The fat/bone index as a sex-differentiating character in man. *Human Biol.*, 21: 199-204.
- SCHJØTZ, C. 1936 Somatologische und funktionelle Untersuchungen an 300 jungen norwegischen Frauen. Oslo.
- SNEDECOR, G. W. 1946 Statistical Methods. Ames, Iowa.
- TANNER, J. M. 1951 Current advances in the study of physique: photogrammetric anthropometry and an androgyny scale. *Lancet*, 1: 574-579.
- WOLFF, G. AND M. STEGGERDA 1943 Female-male index of body build in Negroes and Whites: an interpretation of anatomical sex differences. *Human Biol.*, 15: 127-152.



## THE SEX RATIO OF NEONATAL DEATHS IN JAPAN

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THE number of neonatal deaths by sex and age during 1941 and 1942 was published in "Japanese Vital Statistics" ('41, '42). Since World War II the statistics have been published annually. ("Japanese Vital Statistics," '47, '48, '49). The system of classification of cause of death was altered in 1950.<sup>1</sup> The present observation on the sex ratio of neonatal deaths by age and discussion of causes of death is therefore limited to 1941, 1942, and 1947-1949.

### SEX RATIO OF NEONATAL DEATHS BY DAYS OF AGE

The sex ratio was expressed as the number of males per 100 females. In the calculation of age, deaths on the first day means deaths on the day the baby was born. The sex ratio of neonatal deaths was observed for the first 5 days, every 5 days from the sixth to the thirtieth day, and thereafter, monthly.

The sex ratio of deaths in the first and the second days is between 124-132 as is shown in figure 1. For deaths on the third day the sex ratio is the highest, and it shows almost 140-150. For deaths on the fourth day the ratio decreases and approaches that of the first or the second day. For deaths between the fifth day and the sixth-to-tenth days (1948-1949) or between the fifth day and the eleventh-to-fifteenth days (1941, 1942 and 1947) the ratio diminishes to under 120, but thereafter it usually shows a small rise to 120-130. And then, from about the end of the first month, the ratio falls gradually to the end of the first year.

<sup>1</sup> In Japan parents or relatives register births by notifying the proper authority.





Notwithstanding the fact that the sex ratio of infant deaths after the age of one month varies according to the current of the times, the sex ratio of neonatal deaths shows an almost constant, typical process. The most remarkable feature is the high sex ratio of deaths in the third day, which is shown also in Pfaundler's ('41) data. The calculation of the age by days is done by calendar age in the Japanese manner, therefore, deaths in the third day may include the deaths from 24 hours and a few minutes to about 72 hours.

#### SEX RATIO OF NEONATAL DEATHS BY DIFFERENT CAUSES

It might be expected, if there were a dominant cause of neonatal death with respect to one sex, that the high sex ratio of deaths in the third day would be effected by some specific cause.

The chief causes of neonatal deaths described in vital statistics of 1947-1949 are congenital debility, premature birth, congenital malformation, injury at birth and other diseases peculiar to the newborn and infants, as shown in figure 2. Pneumonia, bronchitis, diarrhea and enteritis, etc., are not as prominent as formerly as the cause of neonatal deaths, especially deaths in the first week.

The total number of deaths in the first day is smaller than in the second or in the third day, since the calculation is done according to calendar age. Congenital debility was always the cause of the most number of deaths in the first month, and the age distribution of deaths for congenital debility is most similar to that of deaths for all causes. The sex ratio of deaths for congenital debility has its peak in the third day, and there is a small rise in the latter half of the first month, as shown in figure 3. For premature births the number of deaths in the third day is not larger than that in the first or in the second day, and the sex ratio of deaths in the third day is not so high as in the first day. The age distribution of deaths for congenital malformation is similar to that for congenital debility, and the sex ratio of deaths for congenital malformation has also a curve similar to that for congenital debility until the end of the first year, but there is a considerable rise in the latter half of the first month. The number of deaths caused by injury at birth diminishes suddenly a few days after birth, but the sex ratio in the third day is the highest of all causes. The number of deaths for other diseases peculiar to the newborn and infants is larger in the third and the fourth days than in other days, and also, the sex ratio is higher in these days.

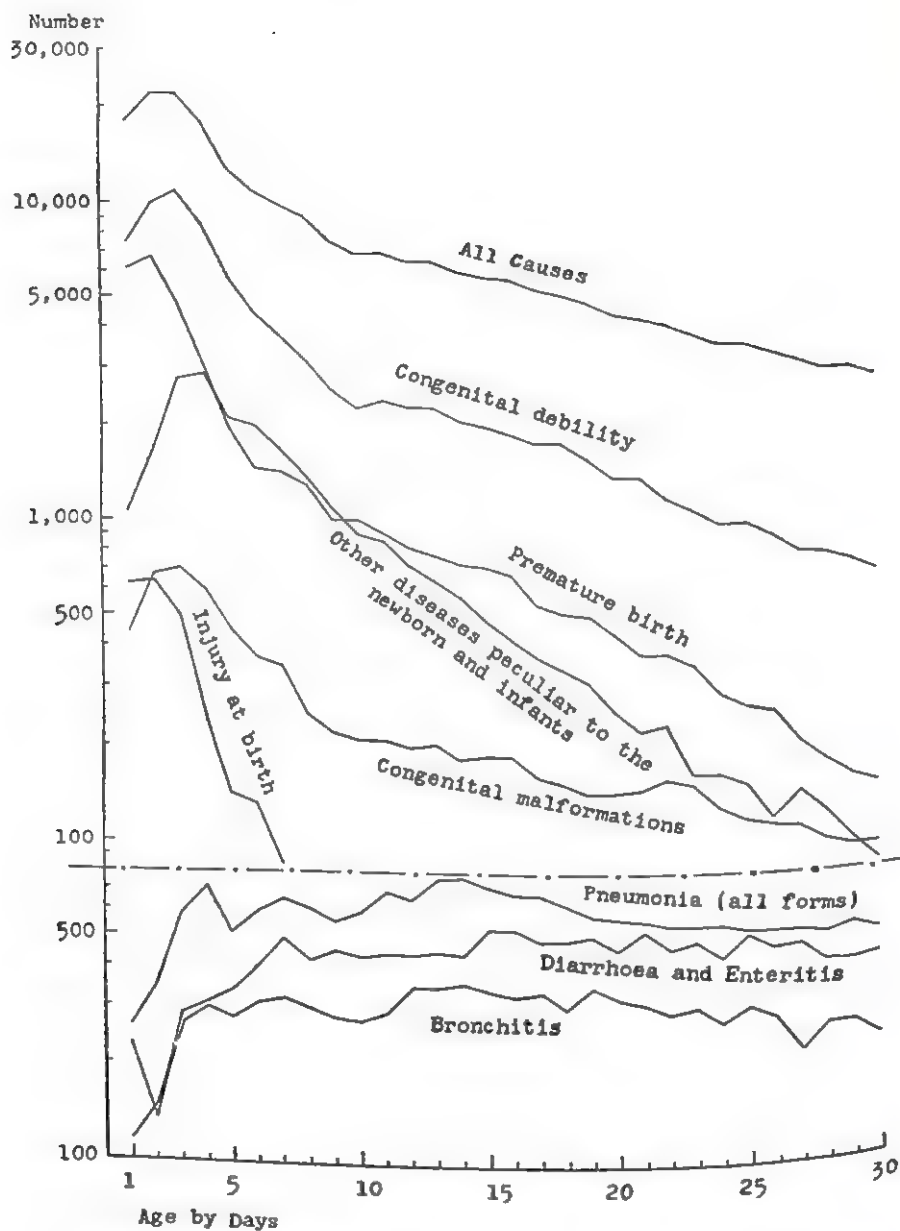


FIG. 2. NUMBER OF DEATHS OF NEWBORN UNDER ONE MONTH BY DAYS RELATED TO SELECTED CAUSES (TOTAL, 1947-49)

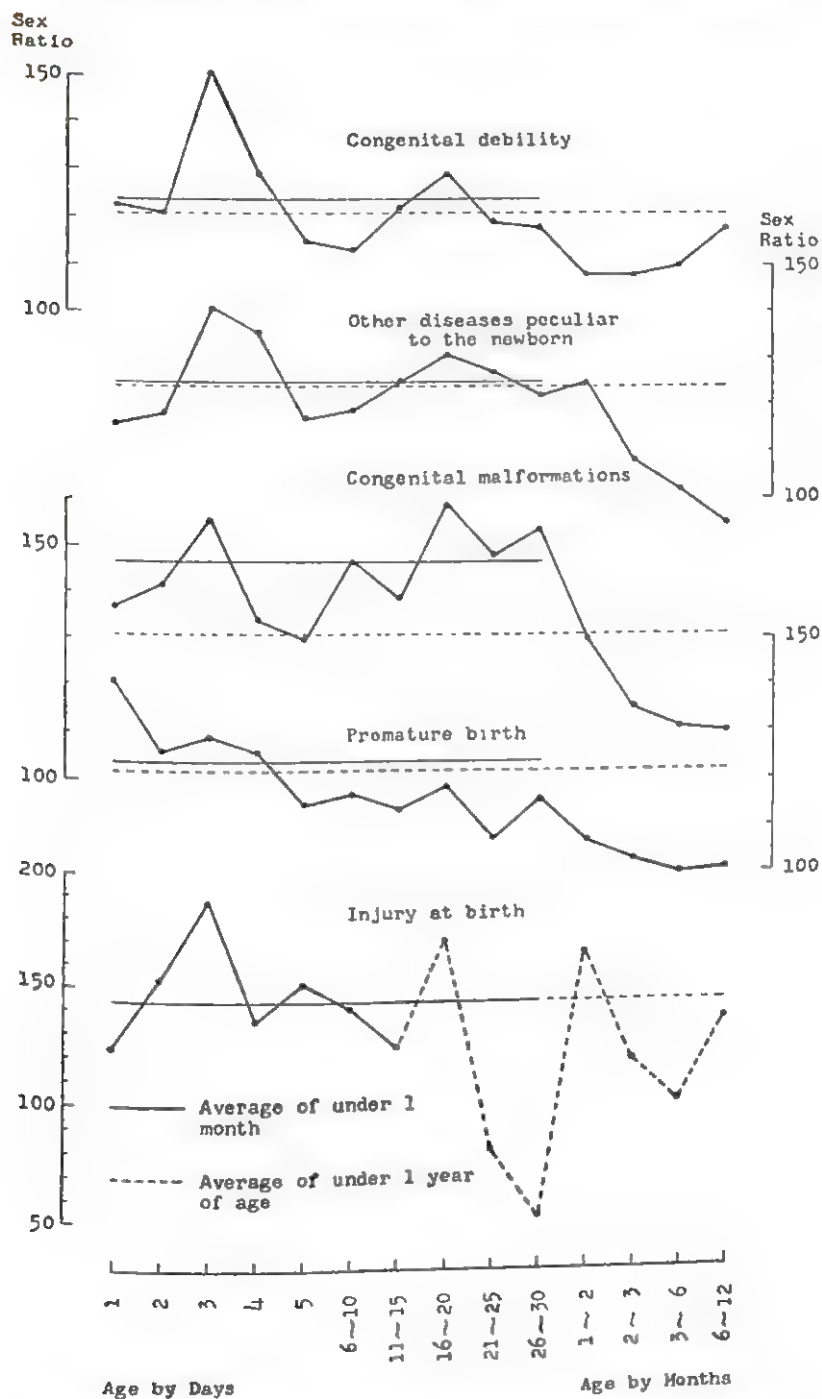


FIG. 3. SEX RATIO OF DEATHS OF INFANTS BY DAYS AND MONTHS RELATED TO SELECTED CAUSES, 1947-1949

The sex ratio of neonatal deaths for most causes, except for premature birth, save a similar type of age distribution. That is, the sex ratio of deaths in the first or second day is not as high as that in the third day; then the ratio shows a rapid decline for some days followed by a gradual rise in the latter half of the first month.

#### DISCUSSION

Neonatal deaths could be considered as the continuation of stillbirths. The fact that the sex ratio of stillbirths rises from the seventh to the ninth month of gestation was recognized by Cioeco ('38) and McKeown and Lowe ('51), in data from the United States and England. The same tendency is also found in Japan (Maruoka, '52). Figure 4 shows the sex ratio of stillbirths by months of gestation from the data of Japanese Vital Statistics of 1939-41. Though the sex ratio of stillbirths under 5 months of gestation seems very high, from 5 to 8 months of gestation the ratio is almost constant at 110-117; and from fetuses of 5 month and over, the percentage of sex unknown falls down under 1%. In the ninth month of gestation the ratio rises significantly to about 126. This sex ratio of stillborn fetuses is very near the sex ratio of neonatal deaths in the first day. The connection of the sex ratio of stillbirth and of neonatal death suggests that these deaths should be understood as perinatal deaths.

Why is the peak of the sex ratio of neonatal deaths in the third day? Here we might examine at first the influence of notification. Different certificates are required in Japan for stillbirths and for live births. Some who die during the first few hours may be listed as stillbirths (thus saving the bother of a second certificate), especially in rural districts. But this is no reason to conclude that the peak of the sex ratio is a cultural rather than a biological phenomenon, since there is no evidence that the deaths of male babies are reported more often as stillbirths than those of female babies. And the same tendency was found by Pfaundler ('42) in data from Bayern, as mentioned above. In the Japanese vital statistics of 1950, in which the age of the newborn was counted for every 24 hours as in the United States, the peak of the sex ratio of neonatal deaths was found in the second and third days.

The causes of neonatal deaths must be examined, although most neonatal deaths are not usually autopsied in Japan. "Congenital debility," which is highest of all causes of neonatal deaths in Japan, is not an exact cause of death. Most Japanese authorities think that "congenital

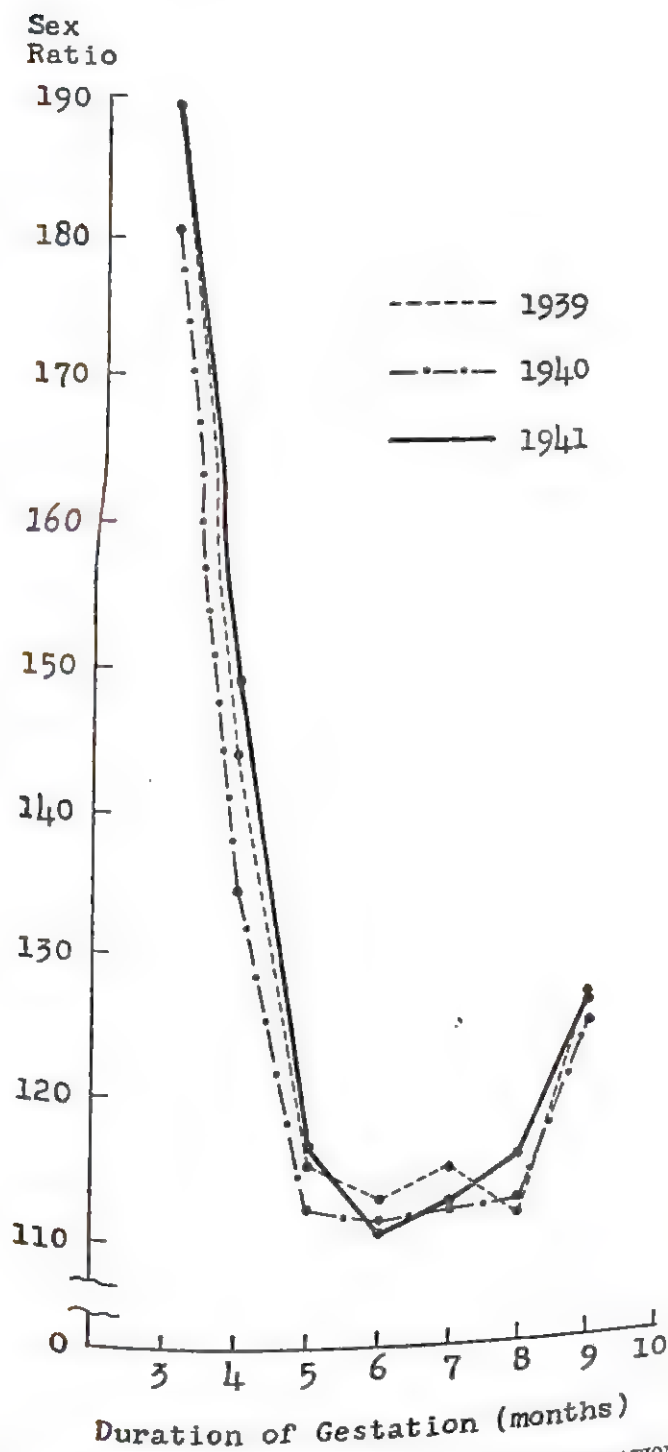


FIG. 4. SEX RATIO OF STILLBIRTHS RELATED TO DURATION OF GESTATION, JAPAN, 1939-1941



debility" must be absorbed in the category of "premature birth." But premature birth, also, is not the actual cause of neonatal deaths as Bundesen ('53) contends. Abnormal pulmonary ventilation seems to be the most important cause as he describes it, though this cause itself might be a result of more fundamental causes. (In this sense "congenital debility" should rather express a real condition.) Anyway, it might be recognized that the absence of the ability to adjust to the new environment at parturition is found more in males than in females. The sex ratio of deaths caused by "premature birth," which must usually be decided in Japan today from the term of parturition or from the weight of the newborn, does not increase sharply on the third day after birth. Therefore premature birth seems to have a qualitative difference from congenital debility. This fact is remarkable.

The diagnosis of "congenital malformation" is given more to those of the newborn who have apparent external malformations rather than to those who have no apparent malformations, because if there are no apparent malformations, internal malformations such as intestinal atresia etc., are not discovered, since most deaths of the newborn are not autopsied. It should be considered that such internal malformations may be included with congenital debility.

If it is a fact that lethal or sublethal genes in the sex chromosome, which manifests itself more in the male than in the female, are the real cause of neonatal deaths, as Lenz ('28, '52) hypothesized, then the high sex ratio of neonatal deaths in the third day might be explained. But, according to Ciocco ('38) and McKeown et al. ('51) the sex ratio of stillbirths for fetal malformation is the lowest. Especially in cases of stillbirth by congenital malformations of the central nervous system such as, anencephalus, spina bifida, etc., is the sex ratio very low as Record and McKeown ('49), McKeown et al. ('51) and MacMahon et al. ('53) recognized. According to MacMahon et al. ('51) in pyloric stenosis of the newborn the sex ratio is very high, but their data is not of deaths but of operated newborns. Since the onset of symptoms of infantile pyloric stenosis is distributed mostly between the first fortnight and the end of the first month, it might be considered that the second smaller rise of neonatal deaths during this period should have some relation to infantile pyloric stenosis. It seems that in Japan today, the chances of diagnosing and operating on cases of infantile pyloric stenosis is less than in England. If there is any congenital obstruction in the digestive tract, the newborn do not live over a few days after birth in the new

environment without operative treatment (Sweetnam et al., '53). Such congenital obstruction might be considered as a cause of the high sex ratio of neonatal deaths in the third day.

"Injury at birth" is a frequent cause of neonatal death, and the sex ratio of neonatal deaths for this cause is the highest in the third day. The cause of the high sex ratio has some similarity with difficult labor as the cause of stillbirths. As the cause of high sex ratio of neonatal deaths for injury at birth, the sexual differences of physical development of the new born might be considered. It might be comprehensible that the male should be injured more by parturition than the female, since the male fetus is, on the average, larger than the female. According to the statistics of 62,000 births from a district in Japan in 1949-50 (Tokano, '51), the body weight of the males is  $3065.9 \pm 2.2$  gm and of the females  $2988.3 \pm 2.2$  gm. But it is questioned whether or not a sexual difference of 77.6 gm could be the cause of the extraordinarily high sex ratio of neonatal deaths in the third day, caused by injury at birth.

It is believed that at present we lack sufficient data to explain the sex ratio of Japanese neonatal deaths in the third day and in the days following.

#### SUMMARY

The sex ratio of neonatal deaths in Japan in 1941, 1942 and 1947-49 was observed by age and by chief causes from government vital statistics data.

The sex ratio of neonatal deaths in the first and second days is near the sex ratio of stillbirths in the ninth month of gestation. The sex ratio of deaths in the third day is the highest, being almost 140-150. In the fourth day and thereafter the ratio decreases and reaches its lowest point between the fifth and the sixth-to-tenth or the eleventh-to-fifteenth days. Thereafter to the end of the first month, the ratio shows a small rise.

The third day's rise of the sex ratio of neonatal deaths, the decline afterwards, and then the small rise in the latter half of the first month were apparent in every chief cause except for premature birth; namely, for congenital debility, congenital malformations, other diseases peculiar to the newborn and infants, and injury at birth.

In order to explain the reasons why the sex ratio of neonatal deaths has this type of progress, we need more data.

## LITERATURE CITED

- BUNDESEN, H. N. 1953 Natal day deaths: the long-neglected field of infant mortality. *J. Amer. Med. Assoc.*, 153: 466-473.
- CIOCCO, A. 1938 The masculinity of stillbirths and abortions in relation to the duration of uterogestation and to the stated causes of foetal mortality. *Human Biol.*, 10: 235-250.
- JAPANESE VITAL STATISTICS 1941, 1942 Bureau of Statistics of the Cabinet, Japan.
- 1947, 1948, 1949 Division of Health and Welfare Statistics, Welfare Minister's Secretariat, Japan.
- LENZ, F. 1928 Erblichkeitslehre und Rassenhygiene. In Halban-Seits, *Biologie und Pathologie des Weibes*, Bd. 1.
- 1952 Ueber Häufigkeit und Bedeutung von Mutationen in menschlichen Populationen. *Homo*, 3: 145-148.
- MACMAHON, B., T. F. PUGH AND T. H. INGALLS 1953 Anencephalus, spina bifida, and hydrocephalus. *Brit. J. Prev. Soc. Med.*, 7: 211-219.
- MACMAHON, B., R. G. RECORD AND T. McKEOWN 1951 Congenital pyloric stenosis. *Brit. J. Soc. Med.*, 5: 185-192.
- MARUOKA, H. 1952 Studies on sex ratio. I. Sex ratio of fetus. *Igaku Kenkyū (Jap.)*, 22: 419-430.
- McKEOWN, T. AND C. R. LOWE 1951 The sex ratio of stillbirths related to cause and duration of gestation. *Human Biol.*, 23: 41-60.
- PFAUNDLER, M. 1942 Studien über Frühföto, Geschlechtsverhältnis und Selektion. IV. Mitteilung. *Z. Kinderheilk.*, 63: 1-132.
- RECORD, R. G. AND T. McKEOWN 1949 Congenital malformations of the central nervous system. I. A survey of 930 cases. *Brit. J. Soc. Med.*, 3: 183-219.
- SWEETNAM, W. P., F. W. SHEPHERD AND E. F. MURPHY 1953 Congenital obstruction of the small intestine in two premature infants. *Brit. Med. J.*, 1: 765-767.
- TAKANO, B. 1951 Statistics of the body-weight of 62,000 newborn babies in Nagano Prefecture in 1949 and 1950. *Eisei Tōkei (Jap.)*, 11: 8-14.





## DIFFERENTIALS IN INFANT MORTALITY BY RACE, ECONOMIC LEVEL AND CAUSE OF DEATH, FOR DETROIT: 1940 AND 1950

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THE wastage of human life has been drastically reduced in those portions of the world where medical and allied sciences have been applied. The greatest progress has been made in the reduction of infant mortality. The unchecked rate of infant mortality is not only high, but extremely variable from year to year, ranging from one-tenth to one-half of all infants born. When infant mortality is controlled as it is in the United States, Western Europe, Australia, and New Zealand, the rate is low, ranging from 20 to 50 per thousand live births, and it fluctuates very little.

The City of Detroit can be classified as an area of very low infant mortality. In 1940 the infant mortality rate in Detroit was 37.43 deaths per thousand live births, while in 1950 it was 27.02 deaths per thousand live births.

Is there a still lower level to which infant mortality may fall, within the framework of existing medical knowledge and practice? This question is immediately answerable, for not only do a number of other places show smaller infant mortality rates,<sup>1</sup> but some groups in Detroit had smaller infant mortality rates in 1950 than the Detroit average. A number of previous studies have shown that infant mortality rate is inversely related to economic level, and that white persons have lower infant mortality rates than nonwhite persons (Collins, '37; Gover, '46; Green, '39; Wiehl, '48; and Woodbury, '25).

<sup>1</sup> Examples of countries having low infant mortality rates in 1950 are: Sweden, 20.5; Iceland, 21.7; New Zealand, 22.7; Australia, 24.5 (United Nations, '52).

In this study, infant mortality rates have been calculated separately for three economic levels and for white and nonwhite persons within each economic level. The total rate has been further subdivided by cause of death, and these causes have been regrouped under three major rubrics: prematurity, physiological causes, and environmental causes. The precise composition of each of these groupings will be explained presently. Data for 1940 and 1950 are shown to illustrate the trend.

#### THE DATA AND METHOD

Our object was to measure as accurately as possible the forces of mortality in the first year of life. This meant a departure from the usual procedure of relating deaths in a calendar year to births in that year. Instead, the births of 1940 and 1950 were related to deaths of infants born during these two years and dying within the calendar year, with the addition of deaths of infants born in 1940 or 1950 and dying in 1941 and 1951 respectively, and the removal of infants born in 1939 and 1949, but dying in 1940 and 1950. Thus, a better approximation of the true probability of death under one year of age was obtained. The probability of death in the first year of life approximates the usual infant mortality rate sufficiently closely under relatively stable mortality and fertility conditions to be roughly comparable, although the two measures are not identical in the strict sense.

The birth and death data were secured from the Detroit Department of Health and are assumed to be very close to a 100% registration. Births and deaths of non-Detroiters were eliminated, and births and deaths of Detroiters occurring in the 4 immediately contiguous counties in Michigan were added. The certificates of the Michigan State Department of Health were used for this purpose. Births and first-year deaths for 1940 totalled 27,141 and 1,016 respectively, while in 1950 these figures were 41,678 births and 1,127 first-year deaths. These totals are slightly below those published in the official reports of the National Office of Vital Statistics, for the reason that some births and deaths occurred outside the 4-county area. However, there is no reason to believe that these few additional births and deaths would significantly change the over-all rates.

The births and deaths were tabulated separately for white and non-white persons, for three broad economic levels based on rentals in the census tract in which the registered individuals lived, and for cause of death.



The method of measuring economic level was comparatively crude, but the major object was to illustrate broad patterns, rather than precise differences. Each birth and death was assigned to a census tract. The census tracts were then grouped into three economic levels by the median monthly rental given in the 1940 census; the class intervals were simply the upper, middle, and lowest thirds of the census tracts arrayed from highest to lowest rental. The same tracts were ascribed to each economic level in 1940 and 1950, the assumption being that the overwhelming majority of census tracts do not change in economic character in a ten-year period. The resulting three economic levels should not be considered as economic or social classes, but only as arbitrary groupings designed to show the presence or absence of an economic gradient. Data for white and nonwhite persons are shown separately by economic level. Although the cash rental levels are equivalent, one cannot assume that the economic level of white and nonwhite persons paying the same rent are equivalent, as nonwhite persons usually pay a larger portion of their total income for rent.

The *Sixth Revision of the International Lists of Diseases and Causes of Death* is currently used by the Detroit Department of Health. Every effort was made to keep the nine pathological categories exactly comparable for the two time periods, 1940 and 1950, since the *Fifth Revision of the Manual of the Causes of Death* was used to code the causes of death in 1940. There were modifications of classifications which affected the definition of causes of infant deaths, but since the Detroit Health Department uses the "intermediate code of the Sixth Revision," the problems created were minimal.

Working from the complete list of causes, we were able to divide all causes of infant deaths into 4 basic groups. "respiratory," "gastro-intestinal," "of early infancy," and "all other." Since this classification was not sharply enough defined for our purposes, we separated all deaths due to prematurity from the "early infancy" group and made prematurity one major category. Next, we took the "congenital malformations," and "all other diseases of early infancy" and made a second major category of causes which we called physiological. In this group we included those deaths of infants from the former "all other" category which were related to a physiological cause, where the condition giving rise to the death arose within the organism. Finally, we united the "gastro-intestinal" causes and the "respiratory" causes, and added the group of "accidental" infant deaths and "birth injury," as well as the

deaths called "all other—environmental," where the cause of death arose from a condition which originated outside the organism. This third major category we called the environmental causes.

#### CHANGES IN THE INFANT MORTALITY RATE 1940-1950

Table 1 indicates the infant mortality rates for the population in general in 1940 and 1950. In 1950 infant deaths from all causes were only 72% of the 1940 level. The greatest reduction occurred in the category of environmental causes. In 1940 there were 12.60 deaths per thousand infants in the environmental group, and in 1950, 7.27 deaths per thousand infants, only 58% of the 1940 rate. Within certain subcategories of the environmental category even more marked changes occurred.

TABLE 1

*Infant mortality rates by cause, Detroit: 1940 and 1950<sup>1</sup>*

	1940		1950		Col. (3) Col. (1)
	(1) Rate	(2) Per cent	(3) Rate	(4) Per cent	
Total	37.43	100.0	27.02	100.0	.72
PHYSIOLOGICAL CAUSES	11.31	30.2	8.93	33.0	.79
Congenital Malformation	5.78	15.4	4.92	18.2	.85
Other Causes of Death in Early Infancy	3.43	9.2	3.17	11.7	.92
All Other, Physiological	2.10	5.6	.84	3.1	.40
PREMATURITY	13.52	36.1	10.82	40.0	.80
ENVIRONMENTAL CAUSES	12.60	33.7	7.27	27.0	.58
Respiratory	4.68	12.6	2.23	8.5	.49
Gastro-Intestinal	1.88	5.0	.77	2.8	.41
Accidents	.55	1.5	.62	2.3	1.13
Birth Injuries	3.83	10.2	3.17	11.8	.83
All Other, Environmental	1.66	4.4	.43	1.6	.26

<sup>1</sup> In this and succeeding tables only the rates per thousand are shown. The number of deaths upon which each rate is based can be computed, for the denominator is always 27,141 births in the case of the 1940 rates, and 41,678 births in the case of the 1950 rates.

"Gastro-intestinal" and "respiratory" causes of infant death were reduced to 41% and 49% of their 1940 levels respectively. The category

"all other" was only 26% of its 1940 level in 1950. The latter probably reflects, among other things, improvements in the degree of care taken when filling out and coding death certificates.

Death rates in two of the major groupings, those of physiological causes and of prematurity, also were reduced in this decade. Each declined to about four-fifths of its 1940 level. Considering that some infants are born, live long enough to breathe, and yet are so grossly malformed or so premature that sustained life is highly improbable, the decline of the infant mortality rate in these categories during the 1940-1950 period reflects a high standard of medical care. There doubtless will be even more improvement in medical techniques in the future, especially in those related to saving the lives of premature infants.

Regarding the proportion of all deaths in 1940, in each of the major categories, deaths due to environmental causes comprised 34% of all deaths in the first year of life, whereas in 1950 they were only 27%.

The purpose of the remaining sections of this paper is to analyze the share of the various groups in the population in the general reduction in infant mortality.

#### WHITE AND NONWHITE POPULATION

Nonwhite persons have always been at a disadvantage compared to white persons in receiving health and medical care. Their life expectancy has been lower, and above all, their infant mortality rate has been markedly higher than white persons living in the same geographic area.

This phenomenon was evident in Detroit in the past and it still prevails. In 1930, deaths among nonwhite infants were 90 per thousand live births, while among white infants there were 62 deaths per thousand live births. This is a ratio of 1.45 deaths among nonwhites to one death among whites. There has been little change in the relative positions of white and nonwhite persons in this respect in the past 20 years. A considerable decline (from 90 to 35 per thousand in the nonwhite population, and from 62 to 25 per thousand in the white population) occurred, but infant death rates for nonwhite persons were still about 40% higher than for whites after 20 years. This might be ascribed to constitutional or genetic differences, inasmuch as the difference between races has remained almost constant. However, division of the causes of death into the major categories suggests other interpretations.

In 1940 environmental causes of death and death from prematurity were substantially higher among nonwhite persons than among white

TABLE 2

*Infant mortality rates by race and cause, Detroit: 1940 and 1950*

	1940			1950		
	(1) White	(2) Nonwhite	Col. (2) Col. (1)	(3) White	(4) Nonwhite	Col. (4) Col. (3)
Total	35.86	52.30	1.46	25.06	35.40	1.41
PHYSIOLOGICAL	11.45	10.00	.87	8.56	10.40	1.23
Congenital						
Malformation	6.07	3.08	.51	5.18	3.79	.73
Other Causes of						
Early Infancy	3.42	3.46	1.01	2.67	5.31	1.99
All Other,						
Physiological	1.96	3.46	1.77	.71	1.39	1.96
PREMATURITY	12.67	21.54	1.70	10.39	12.52	1.21
ENVIRONMENTAL	11.74	20.76	1.77	6.11	12.39	2.03
Respiratory	4.28	8.46	1.98	1.74	4.55	2.01
Gastro-Intestinal	1.96	1.15	.50	.65	1.26	1.94
Accidents	.57	.38	.67	.56	.89	1.59
Birth Injuries	3.55	6.54	1.84	2.75	4.93	1.79
All Other,						
Environmental	1.38	4.23	3.07	.41	.76	1.85

persons. The death rate from physiological causes was actually lower among nonwhite persons than among white persons. In the category of environmental causes, most of the difference was concentrated in deaths from respiratory diseases and birth injuries. By 1950 the picture had shifted considerably, although the over-all proportion was about the same. But whereas the rate for white infants declined only 2.28 per thousand in 10 years, the decline in rate for nonwhites was 9.02 per thousand. Several factors might explain this substantial difference between races in the reduction in frequency of death of premature infants. First, some infants are just too undeveloped at birth to live more than a few hours or days. As the rate of prematurity for white infants was already quite low in 1940, there was less room for improvement during the decade. Therefore, given the present level of medical knowledge, the white population had fewer "preventable" deaths of premature infants.

The second factor is that a premature baby gets practically the same

care regardless of color, or economic level of the parents, provided it is born in a hospital. In 1950, 97.5% of all infants born in Detroit were born in hospitals, while in 1940 only 77.3% were born in hospitals. Thus, equal levels of care were available to more persons, and differentials in the death rates from prematurity declined markedly.

Substantial differences were observed in the relative positions of white and nonwhite infant death rates between 1940 and 1950 in the environmental category. The rates for white persons declined more than the rates for nonwhite persons. Death from "respiratory," "gastro-intestinal," and "accidental," causes were proportionately greater among nonwhite infants as compared with white infants. One plausible explanation for this is that in the decade 1940-1950, the nonwhite population of Detroit increased 100% while the white population increased only 5%. The majority of the migrants were from the rural South where standards of infant care are greatly below those found in large urban centers in the north. It is highly possible that many of the migrants who gave birth to a baby which subsequently died in its first year of life, may have had little awareness of facilities available for infant care. Also family disorganization, so frequent among migrants, may have mitigated against full use of these facilities.

#### ECONOMIC DIFFERENCES IN THE WHITE POPULATION

When infant mortality from all causes is examined, it is seen that there was a distinct economic gradient in both 1940 and 1950 (table 3). That is, the most favored economic group (Economic Group #3) had the lowest infant mortality rate, the middle economic group (Economic Group #2) the middle rate, and the lowest economic group (Economic Group #1) the highest rate. Also, the relative position of the three economic groups with respect to one another, changed little in the course of the decade. As previously noted, the infant mortality rate for the total population in Detroit in 1950 is characterized as low, yet as the rate of 21.82 per thousand in Economic group #3 indicates, still further improvement may be expected in the future if the two lower economic groups, as in the past, equal the standards attained by the highest economic group a few years previously.<sup>2</sup>

<sup>2</sup> The factor of mother's age is frequently associated with infant mortality. While we do not have direct evidence on infant mortality by birth order or age of mother, births, tabulated by age of mother, indicate that the median age of



TABLE 3

*Infant mortality rates for the white population by economic level and cause,  
Detroit: 1940 and 1950*

	(1) Economic Group 1	(2) Economic Group 2	(3) Economic Group 3	Col. (1) Col. (3)	Col. (2) Col. (3)
<i>1950</i>					
Total	28.11	25.95	21.81	1.29	1.19
PHYSIOLOGICAL	8.75	8.82	8.10	1.08	1.09
Congenital Malformation	5.60	5.66	4.31	1.30	1.31
Other Causes of Early Infancy	2.57	2.50	2.93	.88	.85
All Other, Physiological	.58	.66	.86	.67	.77
PREMATURITY	11.66	11.75	8.45	1.38	1.33
ENVIRONMENTAL	7.70	5.88	5.27	1.46	1.12
Respiratory	2.45	1.69	1.29	1.90	1.31
Gastro-Intestinal	.70	.74	.52	1.35	1.42
Accidents	.70	.51	.52	1.35	.98
Birth Injuries	3.15	2.43	2.85	1.11	.85
All Other, Environmental	.70	.51	.09	7.78	5.07
<i>1940</i>					
Total	41.20	34.87	31.85	1.29	1.09
PHYSIOLOGICAL	12.85	10.13	11.91	1.08	.85
Congenital Malformation	6.43	5.51	6.51	.99	.85
Other Causes of Early Infancy	3.63	2.85	4.02	.90	.71
All Other, Physiological	2.79	1.77	1.38	2.02	1.28
PREMATURITY	11.87	14.07	11.49	1.03	1.22
ENVIRONMENTAL	16.48	10.67	8.45	1.95	1.26
Respiratory	6.15	4.23	2.49	2.47	1.70
Gastro-Intestinal	3.07	1.77	1.11	2.77	1.59
Accidents	.70	.49	.55	1.27	.89
Birth Injuries	4.05	2.95	3.88	1.04	.76
All Other, Environmental	2.51	1.23	.42	5.98	2.93

white mothers in the highest economic group was only 1.4 years higher than mothers in the lowest economic group in 1950, and 2.6 years in 1940. Among nonwhite mothers, age differences between economic groups were less than .4 of a year in both 1940 and 1950.

In the category of physiological causes, in both years, the usual inverse relationship between economic level and infant mortality did not hold. The differences that did occur were very small. What further reductions may occur in the future it is difficult to say. A few deaths from these causes should always occur. Yet in each of the economic groups, there was a smaller infant death rate from physiological causes in 1950 than in 1940, and it is probable that further reductions in rate will take place.

The category of deaths caused by prematurity contains some particularly noteworthy relationships. In 1940, the middle economic group had the highest death rate from prematurity (14.07). This again is an instance where the inverse relationship between infant mortality and economic level did not obtain. The same relationship has been previously observed in a similar study conducted by one of the authors in Chicago (Mayer, '50). There, as in Detroit, white infants in the lowest economic group in 1940 had a lower rate of mortality due to prematurity than infants in the next lowest economic group. In 1950, in Detroit the middle economic group again had the highest rate of deaths from prematurity, but the difference between it and the lowest economic group was too small to permit conclusions. In the highest economic group the rate of prematurity was distinctly smaller, 8.45 in 1950 compared with 11.49 in 1940. This indicates a new level of attainment. If the pattern of the past continues, deaths from prematurity in the lowest and middle economic groups will decrease in the future and reach the level of the highest economic group today, and the rate for the highest economic group will continue to decline even further.

In all economic groups, the deaths from environmental causes are becoming fewer. Even in the short space of 10 years, major gains are evident. In 1950, the lowest economic group had a smaller infant death rate from environmental causes than the highest economic group 10 years previously. Also, the differences between the three economic groups were less in 1950 than in 1940.

#### ECONOMIC DIFFERENCES IN THE NONWHITE POPULATION

In 1940, the total infant mortality rate in the nonwhite population was greater in the high economic group (Economic group #2). Analysis by cause indicates this was due to a higher rate in the prematurity category. While the rate for prematurity in the lower economic level of nonwhite population in 1940 was 17.68, the rate for the higher economic

level among nonwhite persons was 31.55. A possible explanation of this relation, as well as the similar observation in the white population, lies in the greater expenditure of social welfare efforts on the poorest persons in the community. Another related possibility is the reluctance of persons, not in actual poverty, to seek the services of welfare and charitable agencies, thereby exposing themselves (in this case their unborn infants) to paid, but medically inferior services.

TABLE 4

*Infant mortality rates for the nonwhite population by economic level and causes  
Detroit: 1940 and 1950*

	(1) Economic Group 1	(2) Economic Group 2	Col. (1) Col. (2)
<i>1950</i>			
Total	37.31	32.94	1.13
PHYSIOLOGICAL	11.03	10.49	1.05
Congenital Malformation	3.81	4.12	.92
Other Causes of Early Infancy	5.82	4.87	1.20
All Other, Physiological	1.40	1.50	.93
PREMATURITY	12.84	11.61	1.11
ENVIRONMENTAL	13.44	10.84	1.24
Respiratory	4.61	4.49	1.03
Gastro-Intestinal	1.81	.37	4.89
Accidents	1.20	.37	3.24
Birth Injuries	4.82	5.24	.92
All Others, Environmental	1.00	.37	2.70
<i>1940</i>			
Total	51.98	53.50	.97
PHYSIOLOGICAL	11.25	6.85	1.64
Congenital Malformation	3.75	1.37	2.74
Other Causes of Early Infancy	3.75	2.74	1.37
All Other, Physiological	3.75	2.74	1.37
PREMATURITY	17.68	31.55	.56
ENVIRONMENTAL	23.05	15.10	1.53
Respiratory	9.65	5.49	1.76
Gastro-Intestinal	1.61		
Accidents	.54		
Birth Injuries	7.50	4.12	1.82
All Other, Environmental	3.75	5.49	.68

In the physiological and environmental categories, the customary inverse relationship of mortality to economic status obtained. Comparing 1940 with 1950, it is seen that economic differentials were smaller in both categories, declining from a ratio of 1.64 in 1940 to 1.05 in 1950 in the category of physiological causes, and from 1.53 in 1940 to 1.24 in 1950 in the category of environmental causes. This could be expected as, with the exception of the rate of deaths from prematurity, the lower economic group had far higher rates of infant mortality than the higher economic group, and consequently there was more room for improvement.

## THE GENERALITY OF THE FINDINGS

As the data examined here pertain to only one geographic area, the question might well be asked: how does the infant mortality rate in Detroit compare with that in other areas? Table 5 contains data com-

TABLE 5

*Infant mortality rates, Detroit, United States, and selected states by race: 1950<sup>1</sup>*

	INFANT MORTALITY RATE	
	White	Nonwhite
Detroit	25.1	35.4
United States	28.9	47.3
United States—Urban	27.8	46.0
Michigan	27.8	40.9
Michigan—Urban	26.9	39.2
New York	25.0	38.3
New York—Urban	24.8	38.5
Illinois	26.0	40.5
Illinois—Urban	26.3	40.2
Pennsylvania	27.8	47.2
Pennsylvania—Urban	27.2	47.3
California	26.2	34.0
California—Urban	24.5	32.7

<sup>1</sup> Data from Statistical Abstract of the United States ('53).

paring Detroit with the United States and with urban places within other states. The states selected for comparison were chosen for their high level of industrialization and of income. Together, these states contain 34% of the population of the United States.

It is evident from the above table that the infant mortality rate among white persons in Detroit is slightly below the rate of the state of Michigan, while Michigan in turn is slightly below the United States as a whole. Comparison with other large industrial states indicates the representativeness of Michigan. In the nonwhite population the variation is somewhat larger, as the rate is higher and higher infant mortality rates are more variable. While the rates shown here suggest that Detroit is not atypical, generalization of the findings of this study, especially as to the effects of economic differentials, must be made with caution.

#### WHY STUDY INFANT MORTALITY IN AREAS WHERE THE RATE IS ALREADY LOW?

This study indicates that, where infant mortality has reached a low level, little in the way of a major decline in the rate can be expected in the future. While there is still room for improvement, and subsequent advances in medical science (especially in the care of premature infants) will undoubtedly take place, it is doubtful that medical and biological science can learn anything new from further epidemiological study. However, the study of infant mortality will, in the future as in the past, be important to the social scientist. The infant mortality rate has been considered an excellent index of the level of living of a population. This study indicates that, even when the infant mortality rate for a total population is low, as in Detroit today, there are still differences between various subgroups in the population. Although the differences are small, they are consistent. Very probably they will prove extremely persistent, and it may be many years until equally low infant mortality rates are attained by all groups residing in the same area. Until that time, the infant mortality rate can continue to be used as an index of the level of living of various subgroups of the population. Birth and infant death statistics are among the most precise and readily obtained social data, and can be conveniently used to classify groups of persons, or geographic areas in which such groups of persons reside.

#### SUMMARY

(1) Detroit has a low rate of infant mortality (27.02 per thousand live births in 1950). This is a marked decrease from the rate of 37.43 infant deaths per thousand live births in 1940.

(2) The largest reduction in infant mortality was found among those causes grouped under the general heading of "environmental



causes." About 51% of the total reduction of 10.41 per thousand represented a reduction in environmental causes.

(3) Although the infant mortality rates of both white and nonwhite infants declined markedly during the decade 1940-1950, the relative position of the nonwhites improved only slightly, changing from 46% higher than the whites in 1940 to 41% higher than the whites in 1950.

(4) Infant mortality rates in the white population of Detroit in both 1940 and 1950 were, as usual, inversely proportional to economic level. However, when subclassified by cause of death, the usual pattern did not apply in 1940, since the middle economic group had a higher rate of deaths due to prematurity than did either the highest or the lowest economic group. This was equally true in the nonwhite population. A greater use of social welfare facilities on the part of the lowest economic group is a suggested cause of this.

(5) Deaths from environmental causes reached very low levels in all white economic groups in 1950. Although slight economic differences persisted, the margin of difference between economic groups in the white population was less in 1950 than in 1940.

(6) In general, the relationship between similar economic groups in the nonwhite population was as in the white population.

### LITERATURE CITED

- BULLETIN DETROIT DEPARTMENT OF HEALTH 1940 City Health. Annual Report 25: (1).
- 1950 City Health. Annual Report 35: (1).
- COLLINS, SELWYN D. 1927 Economic Status and Health; A Review and Study of the Relevant Morbidity and Mortality Data. U. S. Public Health Service, Public Health Bulletin Number 165, Washington, D. C.
- GOVER, MARY 1946 Negro mortality. II. The birth rate and infant and maternal mortality. Public Health Reports, 61: 1529-1538.
- GREEN, H. W. 1939 Infant Mortality and Economic Status; Cleveland Five City Area, 1919-1937. Cleveland Health Council, Cleveland.
- MAYER, A. J. 1950 Differentials in length of life, City of Chicago: 1880-1940. Unpublished Ph. D. dissertation. University of Chicago Libraries.
- STATISTICAL ABSTRACT OF THE UNITED STATES 1953 United States Department of Commerce, Washington, D. C.
- WIEHL, D. G. 1948 Mortality and socio-environmental factors. Milbank Memorial Fund Quarterly, 26: 335-365.
- WOODBURY, ROBERT M. 1925 Causal Factors in Infant Mortality. U. S. Children's Bureau, Publication Number 142, Washington, D. C.
- UNITED NATIONS DEMOGRAPHIC YEARBOOK 1952 Statistical Office of the United Nations, New York.



# THE EFFECT OF BIRTH WEIGHT AND TIME OF FIRST FEED ON THE WEIGHT OF BANTU BABIES IN THE FIRST 10 DAYS OF LIFE

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THE weights of Bantu babies in the first 10 days of life, with special reference to rank order of birth, sex and marital status of mothers have been reported upon previously (Salber and Bradshaw, '53). In this paper we are concerned with the effect on their subsequent growth of (1) the birth weight of babies and (2) the time of first feed after birth.

## MATERIAL AND METHOD

The same babies were used in this study as described in the previous paper, *i. e.* 598 full-term babies, born of normal vertex delivery, who were well during their stay in hospital. For this study it was necessary to have the birth weight of the baby, and also the time at which the baby was first put to the breast. Where this information was not available the cases were discarded, leaving us with 596 babies of known birth weight, and 577 babies whose time of first feed was recorded.

The babies were divided into three birth weight groups, *i. e.* 5 lb. 8 oz. to 6 lb. 7 oz., 6 lb. 8 oz. to 7 lb. 15 oz., and 8 lb. and over, and their progress was compared.

With regard to the time of first feed after birth, we planned to compare three groups, *viz.*: those fed as soon after birth as possible, those fed as late after birth as possible, and those in between. However, we soon found that this interfered with the hospital routine to a large

<sup>1</sup> Senior Bursar of the Council for Scientific and Industrial Research at the time the data for this study was collected and the analysis completed.

extent and, although it was possible to have babies fed soon after birth, it was extremely difficult to have the first feed delayed much longer than 10 hours. As a result the three feeding groups are:

1. Those fed within the first hour (59 minutes or less).
2. Those fed between 1 and 6 hours after birth (1 hour to 5 hours 59 minutes).
3. Those fed 6 or more hours after birth (6 hours or more).

The distribution of the times of the first feed in single hours is shown in appendix 1.

As in the previous paper, daily gains or losses from birth weight were calculated, also the total initial loss and the duration of loss. This was done for the three birth weight groups and the three feeding groups, sexes and ranks separately.

## RESULTS

### *The effect of birth weight on loss of weight after birth*

*Mean daily loss in weight.* Longridge ('05), Griffith and Gittings ('07) and Martin ('31) found that the heavier the baby, the more weight is lost. Hammett ('18) and Meredith and Brown ('39) found the loss for heavy infants to be both absolutely and relatively greater than for light infants, but Ramsey and Alley ('18) and Naish and Edwards ('52) found no difference in percentage weight loss.

Our babies were divided into three birth weight groups as previously stated, and will be referred to as light, average and heavy babies.

Since birth rank has a marked influence on weight loss after birth—first babies losing more weight than later born babies—Salber and Bradshaw ('53), we investigated separately first-born (Rank 1) and subsequently-born (Rank 2+). Our results show that the heavier babies tend to lose more weight, both actual and relative, than the light babies (appendix 2). Further, in Rank 1 the heavier babies lose for a day longer than the lighter babies. In Rank 2+, however, all the babies lost for the same time (two days) except for the light boys, who inexplicably lost for three days.

*Total initial loss.* As mentioned in the previous paper, not all the babies reached their minimum weight on the third day, and it was necessary to examine the mean amount of weight lost regardless of when this occurred. A decided difference in the total initial loss was found,

with the heavier babies losing more actual weight. This applied to both sexes, and to Ranks 1 and 2+ separately. The relative loss of weight, expressed as a percentage of birth weight, showed little difference between the birth weight groups, and these results were not consistent (appendix 3). The heavier babies lost for a slightly longer period, but the differences were very small (appendix 4).

*The effect of birth weight on regain of weight*

Hammett ('18) reported that "the lighter the initial weight, the earlier the recovery of weight loss." Martin ('31), however, found no difference in the weight gain of lighter or heavier babies. Meredith and Brown ('31) stated that the actual gain was more for light babies.

*Gain.* As some birth weight groups had no information after the seventh day, investigation into the weight gain had to be limited to the first 4 days after the day of minimum weight. Table 1 shows the actual

TABLE 1

*Gain in 4 days from minimum weight*

	RANK 1				RANK 2+			
	Girls		Boys		Girls		Boys	
	Amount	%	Amount	%	Amount	%	Amount	%
Birth Weight Groups:								
Light	1.74 oz	1.8	4.38 oz	4.6	3.76 oz	3.9	4.05 oz	4.2
Average	3.19 "	2.8	5.69 "	5.0	3.73 "	3.2	4.45 "	3.8
Heavy	—	—	—	—	3.53 "	2.4	4.89 "	3.6

amount of gain in those 4 days, and also the relative amount, as a percentage of birth weight. It can be seen that Rank 1 is quite consistent, and for both girls and boys average babies gain more actual and more relative weight than light babies. In Rank 2+ the picture is different—for both girls and boys the relative weight gain is greatest for the light babies and smallest for the heavy babies. In actual amount of gain, however, while the light girls gain the most, it is reversed for the boys, with the heavy babies gaining the most.

*Return to birth weight by seventh day.* The percentage of babies who had regained birth weight by the seventh day is the resultant of

1. The amount of weight lost.
2. The duration of that loss.
3. The rate of gain thereafter.

In Rank 1 girls a greater percentage of the light babies had regained their birth weight than the average babies, whereas for the boys there is a very slight difference in the opposite direction. In Rank 2+ the lighter girls again do very much better than the heavier girls, whereas the average boys do better than the rest. (See appendix 5).

*Day on which group returned to birth weight.* This is only applicable to Rank 2+ babies. (See appendix 2). Here again the light girls did better than the rest, for although both light and average babies had regained their birth weight by the eighth day, the light babies were 1.9 oz over birth weight, whereas the average girls were only .5 oz over birth weight. The average boys again did better than the other groups, regaining birth weight by the seventh day. As the groups in Rank 1 had not regained birth weight, we compared seventh day losses as a percentage of birth weight. In both girls and boys the light babies were closer to birth weight than the average babies.

The effect of birth weight, then, on loss and gain of weight after birth shows no clear pattern. Results vary both for the ranks and the sexes. We decided therefore, in an endeavor to obtain a clearer picture, to score the groups for the categories previously mentioned:

1. Day of maximum loss.
2. Amount of loss as a percentage of birth weight.
3. Total initial loss as a percentage of birth weight.
4. Duration of loss.
5. Gain in 4 days after minimum weight.
6. Percentage who regained birth weight by the seventh day.
7. Day on which group returned to birth weight.

*Whichever group did best in each category was given one point, and in the event of two or three groups doing equally well, they each scored one point.*

It is obvious from table 2 that the light girls do better than the others both in Rank 1 and Rank 2+. Light boys do better in Rank 1, but average boys do best in Rank 2+.



TABLE 2

*Comparison of three birth weight groups with respect to various factors.  
Sexes and ranks separately.*

	RANK 1														RANK 2+														
	Girls							Boys							Girls							Boys							
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	
Light	1	1	1			1	1	1	1	1			1	1	1	1	1	1	1	1						1	1		
Average				1	1					1	1	1			1								1	1	1	1		1	1
Heavy															1								1						

It is still a fact, however, that because of their superior birth weight, the heavy babies retain their lead (as far as actual weight is concerned) over the average and light babies on discharge from hospital.

*The effect of time of first feed after birth on the progress of the babies*

The three feeding groups (called hereafter early, middle and late) were examined with regard to loss and gain in weight in the same way as the birth weight groups were done. One of the 7 categories (gain in 4 days after minimum weight) was omitted because of insufficient data. (See appendices 3, 4, 5 and 6).

*Mean daily loss in weight.* In Rank 1 babies, the girls of the late feeding group lost less percentage weight than the middle group, with the same duration of loss (appendix 6; insufficient data for early feeders). In the boys, the middle feeders did better—both for percentage weight loss and duration of loss than the early feeders (insufficient data for late feeders). In Rank 2+, for both boys and girls the middle feeding group were best with regard to percentage loss of weight, and the middle and late feeding girls lost for a shorter period than the early feeding girls. However, the early feeding boys lost for the shortest time.

*Total initial loss of weight.* In Rank 1 the late feeding girls and the middle feeding boys did best, whereas in Rank 2+ the middle feeding girls and the early feeding boys did best. The duration of this loss of weight follows almost exactly the same pattern as the total initial loss (appendices 3 and 4).

*Return to birth weight.* In Rank 1 the middle feeding girls and boys, and in Rank 2+ the middle feeding girls and the early feeding

boys were superior in the percentage who had regained their birth weight by the seventh day (appendix 5). With regard to the day on which the group returned to birth weight, there was insufficient data for Rank 1. In Rank 2+ the middle feeding girls and the early feeding boys returned to birth weight soonest.

Here again the picture is not clear, and we followed the same scoring procedure as before, with the omission of the one criterion mentioned previously. Table 3 shows quite an interesting pattern: in Rank 1 it appears that late feeding girls and middle feeding boys progress most favorably, and the same applies to middle feeding girls and early feeding boys in Rank 2+.

TABLE 3

*Comparison of three feeding groups, with respect to various factors.  
Sexes and ranks separately.*

	RANK 1										RANK 2+													
	Girls					Boys					Girls					Boys								
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
59 minutes or less																			1		1	1	1	1
1-5 hours	1				1		1	1	1	1	1	1	1	1	1	1	1	1		1				
6 hours or more	1	1	1	1									1										1	

## DISCUSSION

The birth weight of the baby and the time of first feed after birth have some effect on the progress of the baby in the first 10 days of life, although these factors are not nearly as strong as the factor of rank order.

The effect of birth weight on progress after birth is slight. With regard to mean daily loss of weight the heavier babies lose more actual and relative weight than the lighter babies, and on the whole for a longer period. The total initial loss is also greater for heavier babies, although the relative loss is much the same. As far as the effect of birth weight on gain after birth is concerned, the average Rank 1 babies gain the most relative and absolute weight. In Rank 2+ the light babies gain most relative weight, but the actual amount of weight gained varies for boys and girls. On the whole the light girls and the average boys returned to birth weight soonest, and a greater percentage of babies in these two groups had regained birth weight by the seventh day.

When each category was scored, the total progress picture showed

that for girls in Rank 1 and Rank 2+ the light babies did best. For boys differed with the ranks—light boys being better off in Rank 1 and average boys in Rank 2+.

As mentioned previously, although the heavy babies lose more weight, and do not gain as much as the light and average babies, they are still the heaviest group on discharge from hospital owing to their superior birth weight. Various investigators have studied the effect of birth weight on subsequent growth. Illingworth et al. ('49) found that throughout childhood the average child who was a small baby at birth weighed considerably less than the average child who at birth was a large baby. Lowe and Gibson ('53) stated that "the mean weight at the third birthday is closely related to the birth weight." Parfit ('51), however, points out that the actual amount of weight gain is the same for the different birth weight groups after the first month, and Hammond ('52) also found that birth weight appeared to have no effect on weight gain in the first year. This means, in effect, that heavier babies at birth remain heavier subsequently, but that smaller babies gain more relative weight than larger babies, since the actual increments are the same.

The time of first feed after birth has a greater effect on subsequent progress than has birth weight. In Rank 1, for all measures of loss of weight and the duration of that loss, the late feeding girls and the middle feeding boys had the advantage. In Rank 2+, the middle feeding girls were unequivocally superior to the other groups. The differences were not as striking in the boys, although there was a tendency for the early feeding group to lead. The middle feeding girls and the early feeding boys in Rank 2+ also returned to birth weight soonest, while in Rank 1 both boys and girls of the middle feeding group did best.

When the categories were scored, an interesting pattern emerged (table 3). Second and later born babies could advantageously be fed earlier than first-born babies, and boys could be fed earlier than girls.

A very tentative explanation for these findings may be that Bantu boys recover more quickly from the stress of labor than Bantu girls, and that second and later born babies are less affected than first born babies.

We could find no reference in the literature to the effect of time of first feed after birth on the subsequent progress of the babies. Enquiries at the leading maternity hospitals and nursing homes in Durban revealed that the routine time of first feed after birth varied from three to 12 hours, with no definite reasons given for the time interval chosen. Various obstetric and baby-feeding textbooks in England and America

give time of first feed after normal delivery to be anything between 8 and 24 hours after birth, the reasons being to allow the mothers and babies to recover from the effects of labor. It would appear that investigation in this field is necessary if we are to have any scientific reason for a particular time interval between birth and first feed.

#### SUMMARY AND CONCLUSIONS

Five-hundred and ninety-eight full term babies, born of normal vertex delivery, who were well during their stay in hospital, were studied with reference to the effect of birth weight and the time of first feed on their progress in the first 10 days of life.

(a) The effect of birth weight was slight.

1. In all ranks heavier babies lost more actual and relative weight than lighter babies, and on the whole for a longer period.
2. In first born (Rank 1), the average babies gained more absolute and relative weight than the light babies.
3. In subsequent births (Rank 2+), the light babies gained most relative weight, although the actual weight gain varied for boys and girls.
4. In all ranks the light girls and the average boys returned to birth weight soonest.
5. The total progress showed that light girls did best in all ranks. Light boys were better off in Rank 1, and average boys in Rank 2+.

However, owing to their superior birth weight, heavy babies still weighed the most on discharge from hospital.

(b) Time of first feed after birth had a greater effect on subsequent progress than did birth weight.

1. In Rank 1, late feeding girls and middle feeding boys lost less weight, and for a shorter period than the other groups, while in Rank 2+, middle feeding girls and early feeding boys had the smallest loss.
2. In Rank 1, middle feeding girls and boys returned to birth weight soonest, while in Rank 2+ middle feeding girls and early feeding boys were superior.

3. The total progress picture showed that second and later born babies could be fed earlier than first born, and boys could be fed earlier than girls.

With the exception of first-born girls, babies were best off being fed within 6 hours of birth.

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#### LITERATURE CITED

- GRIFFITH, J. P. C. AND J. C. GITTINGS 1907 The weight of breast-fed infants during the first two weeks of life. *Arch. Pediat.*, 24: 322-347.
- HAMMETT, F. S. 1918 The effect of the maternal ingestion of dessicated placenta upon the rate of growth of breast-fed infants. *J. Biol. Chem.*, 36: 569-573.
- HAMMOND, W. H. 1952 Some observations on the conditions affecting the first year growth of babies. *Medical Officer*, 88: 225-228.
- ILLINGWORTH, R. S., C. C. HARVEY AND SHAN-YAH GIN 1949 Relation of birth weight to physical development in childhood. *Lancet*, 2: 598-603.
- LONGRIDGE, C. N. 1905 The initial loss of weight in infants. *Brit. Jour. Child. Dis.*, 2: 403-407.
- LOWE, C. R., AND J. R. GIBSON 1953 Weight at third birthday related to birth weight, duration of gestation and birth order. *Brit. J. Prev. Soc. Med.*, 7: 78-82.
- MARTIN, W. J. 1931 A biometric study of the weights of infants, during first days of life. *Ann. Eugen.*, 4: 327-338.
- MEREDITH, H. V., AND A. W. BROWN 1939 Growth in body weight during the first ten days of postnatal life. *Human Biol.*, 11: 24-77.
- NAISH, F. C., AND P. W. EDWARDS 1952 Initial weight loss: a preliminary enquiry. *Arch. Dis. Child.*, 27: 445-448.
- PARFITT, J. 1951 A study of weight gain in the first year of life. *Brit. J. Prev. Soc. Med.* 5: 1-12.
- RAMSEY, W. R., AND A. G. ALLEY 1918 Observations on the nutrition and growth of newborn infants. *Amer. J. Dis. Child.*, 15: 408-412.
- SALBER, E. J. AND E. S. BRADSHAW 1953 Weight of Bantu babies in the first ten days of life. *Brit. J. Prev. Soc. Med.*, 7: 154-159.



APPENDIX 1  
*Distribution of times of first feed*

HOURS AFTER BIRTH	BOYS		GIRLS	
	Rank 1	Rank 2+	Rank 1	Rank 2+
0	21	68	18	68
1	13	25	11	34
2	16	21	7	22
3	7	14	6	28
4	3	14	5	11
5	2	13	4	9
6	2	9	3	9
7	5	10	2	7
8	2	10	5	10
9	1	11	3	8
10	3	10	2	6
11	..	1	2	1
12	..	..	3	..
13	..	1	..	..
14	..	1	..	2
15	1	1	..	..
16	..	..	..	..
17	..	..	..	..
18	..	1	..	..
19	..	1	..	..
20	..	..	..	..
21	..	..	1	..
22	..	1	..	1
27	..	..	..	1

APPENDIX 2 (a)  
*Mean daily gain or loss in weight in ounces according to birth weight—girls*

Rank 1

DAY	6 LB 7 OZ OR LESS			6 LB 8 OZ-7 LB 15 OZ			8 LB OR MORE		
	NO	MEAN	SD	NO	MEAN	SD	NO	MEAN	SD
1	26	-1.73	1.78	33	-2.89	2.26	6	.	.
2	30	-4.00	1.65	37	-5.58	2.94	6	.	.
3	30	-5.20 (5.4%)	3.48	38	-7.21	5.29	6	.	.
4	30	-5.13	5.21	38	-7.37 (6.4%)	6.77	6	.	.
5	29	-4.86	5.58	37	-6.51	7.87	6	.	.
6	28	-4.07	6.33	36	-5.78	8.70	6	.	.
7	26	-3.46 (-3.6%)	6.64	32	-5.44 (-4.7%)	9.38	5	.	.
8	17	..	..	22	-4.18	10.61	5	.	.
9	13	..	..	15	..	..	3	.	.
10	5	..	..	3	..	..	1	.	.

Rank 2+

DAY	6 LB 7 OZ OR LESS			6 LB 8 OZ-7 LB 15 OZ			8 LB OR MORE		
	NO	MEAN	SD	NO	MEAN	SD	NO	MEAN	SD
1	41	-2.26	2.03	123	-2.44	2.39	29	-3.40	3.37
2	56	-4.20 (4.3%)	2.69	132	-5.64 (4.9%)	3.27	34	-6.59 (4.8%)	3.21
3	56	-4.04	4.11	133	-5.63	4.61	34	-6.06	4.37
4	55	-2.64	5.63	131	-4.33	5.36	34	-4.47	5.62
5	54	-1.81	6.52	129	-2.84	6.23	34	-3.35	6.73
6	54	-0.44	6.95	125	-1.91	6.89	34	-3.06	7.66
7	46	-0.30	7.42	107	-0.51	7.75	30	-1.47	7.84
8	28	+1.86	8.02	68	+0.53	7.91	17	..	..
9	15	..	..	33	-0.27	7.42	11	..	..
10	7	..	..	11	..	..	4	..	..

## APPENDIX 2 (b)

*Mean daily gain or loss in weight in ounces according to birth weight—boys*

Rank 1

DAY	6 LB 7 OZ OR LESS		6 LB 8 OZ-7 LB 15 OZ		8 LB OR MORE	
	NO	MEAN	NO	MEAN	NO	SD
1	25	-2.62	37	-2.58	8	3.06
2	27	-5.59	41	-5.93	9	3.78
3	27	-6.56 (6.9%)	41	-8.32	10	5.16
4	27	-6.26	40	-8.45 (7.4%)	10	6.71
5	27	-5.07	40	-7.60	10	8.16
6	25	-4.84	40	-6.05	10	8.40
7	22	-2.18 (2.3%)	38	-5.05 (4.4%)	10	8.94
8	16	..	33	-2.76	8	8.54
9	9	..	25	-0.12	7	8.16
10	5	..	10	..	3	..

Rank 2+

DAY	6 LB 7 OZ OR LESS		6 LB 8 OZ-7 LB 15 OZ		8 LB OR MORE	
	NO	MEAN	NO	MEAN	NO	SD
1	24	-2.00	116	-2.41	48	2.87
2	28	-4.07	133	-5.10 (4.4%)	55	-6.65 (4.9%)
3	29	-4.38 (4.5%)	134	-4.70	56	-6.01
4	29	-3.69	133	-3.33	56	-5.11
5	29	-2.52	134	-1.73	54	-3.59
6	28	-1.50	131	-0.65	55	-1.76
7	24	-0.33	109	+0.03	46	-0.83
8	15	..	70	+1.37	32	+1.19
9	8	..	31	+2.29	18	..
10	2	..	12	..	9	..

## APPENDIX 3

Total initial loss of weight (in ounces)

	RANK 1			RANK 2+			RANK 2+		
	NO	GIRLS MEAN	SD	NO	BOYS MEAN	SD	NO	GIRLS MEAN	SD
<i>Birth Wt Groups</i>									
6 lb 7 oz or less	30	7.00 (7.3%)	3.94	27	8.54 (8.9%)	4.45	56	5.73 (5.8%)	3.56
6 lb 8 oz-7 lb 15 oz	38	9.11 (7.9%)	6.07	41	10.13 (8.9%)	6.35	132	7.32 (6.4%)	4.32
8 lb or more	6	..	..	10	..	..	34	8.03 (5.9%)	4.93
<i>Time of First Feed after Birth</i>									
59 minutes or less	18	..	..	21	10.98	5.47	68	7.87	4.70
1-5 hours	33	9.05	5.54	41	9.16	6.01	104	6.47	4.12
6 hours or more	21	7.17	4.31	14	..	..	45	7.23	3.97
							57	6.94	4.58
							68	6.62	3.50
							87	7.01	4.28
							57	6.94	4.58

## APPENDIX 4

Duration of loss of weight in days

	RANK 1			RANK 2+			RANK 2+		
	NO	GIRLS MEAN	SD	NO	BOYS MEAN	SD	NO	GIRLS MEAN	SD
<i>Birth Wt Groups</i>									
6 lb 7 oz or less	30	3.70	1.49	27	3.46	1.14	56	3.00	1.13
6 lb 8 oz-7 lb 15 oz	38	3.63	1.70	41	3.74	1.30	132	3.09	1.23
8 lb or more	6	..	..	10	..	..	34	3.12	1.35
<i>First Feed</i>									
59 minutes or less	18	..	..	21	3.98	1.53	68	3.18	1.25
1-5 hours	33	3.99	1.74	41	3.38	1.09	104	2.94	1.12
6 hours or more	21	3.60	1.51	14	..	..	45	3.23	1.44
							57	2.87	1.89
							68	2.90	1.96
							87	3.02	1.04
							57	2.87	1.89
							68	2.90	1.96
							87	3.02	1.04
							57	2.87	1.89





## APPENDIX 6 (a)

*Mean daily gain or loss in weight in ounces according to time of first feed after birth*

Girls: Rank 1

DAY	59 MINUTES OR LESS		1-5 HOURS		6 HOURS OR MORE	
	NO	MEAN	NO	MEAN	NO	SD
1	17	..	28	-2.57	19	..
2	18	..	33	-5.29	20	-4.85
3	18	..	33	-6.52	21	-6.02
4	18	..	33	-6.70 (6.1%)	21	-6.24 (5.6%)
5	17	..	33	-5.55	20	-5.80
6	17	..	33	-4.82	18	..
7	14	..	29	-4.66	18	..
8	13	..	17	..	12	..
9	8	..	13	..	8	..
10	2	..	5	..	2	..

Girls: Rank 2+

DAY	59 MINUTES OR LESS		1-5 HOURS		6 HOURS OR MORE	
	NO	MEAN	NO	MEAN	NO	SD
1	55	-3.06	90	-2.19	43	-2.57
2	67	-5.95	103	-5.02 (4.3%)	45	-5.79 (4.9%)
3	67	-6.16 (5.3%)	104	-4.67	45	-5.41
4	67	-5.00	102	-2.84	44	-4.50
5	66	-3.61	99	-1.69	45	-2.91
6	64	-2.78	99	-0.64	43	-2.12
7	56	-2.18	87	+0.56	37	-0.73
8	32	-0.44	56	+1.68	22	0.00
9	10	..	33	+2.52	15	..
10	3	..	11	..	7	..

## APPENDIX 6 (b)

## Boys: Rank 1

DAY	59 MINUTES OR LESS		1-5 HOURS		6 HOURS OR MORE	
	NO	MEAN	SD	NO	MEAN	SD
1	16			39	-2.03	3.32
2	21	-6.71	4.20	40	-5.95	3.95
3	21	-8.14	4.39	41	-7.39 (6.6%)	5.18
4	21	-8.33 (7.5%)	4.71	40	-6.80	6.71
5	21	-7.48	5.98	40	-5.95	7.95
6	21	-7.00	6.82	38	-4.89	7.87
7	20	-6.20 (5.6%)	7.55	37	-3.11 (2.8%)	8.33
8	17	..	..	30	-1.73	7.91
9	15	..	..	18	..	..
10	5	..	..	8	..	..

## Boys: Rank 2+

DAY	59 MINUTES OR LESS		1-5 HOURS		6 HOURS OR MORE	
	NO	MEAN	SD	NO	MEAN	SD
1	58	-2.97	2.53	74	-2.72	2.94
2	68	-5.44 (4.6%)	2.87	84	-5.19	2.95
3	69	-5.14	3.58	86	-5.31 (4.4%)	4.15
4	69	-3.38	4.82	85	-4.11	5.82
5	69	-1.81	5.35	85	-2.60	6.28
6	67	-0.13	6.15	85	-1.19	6.45
7	57	+0.82	6.18	71	-0.10	6.96
8	37	+3.54	6.49	47	+1.04	6.26
9	17	..	..	23	+3.00	6.21
10	9	..	..	8	..	..

Figures in parentheses show percentage of birth weight lost by day of maximum loss; and also, for purposes of comparison, on 7th day where no information is available as to when the group regained its birth weight.

## BOOK REVIEWS

*Anthropology Today: An Encyclopedic Inventory.* Prepared under the chairmanship of A. L. KROEBER, Pages xvi + 966, University of Chicago Press, 1953, \$9.00.

*An Appraisal of Anthropology.* Edited by SOL TAX, LOREN C. EISELEY, IRVING ROUSE, and CARL F. VOEGELIN, Pages xiv + 395, University of Chicago Press, 1953, \$6.00.

For two weeks, from 9 to 20 June 1952, some eighty scholars, most of whom were anthropologists, conducted an international symposium on anthropology. The symposium was initiated and held under the generous auspices of the Wenner-Gren Foundation for Anthropological Research. The theme of the symposium was "A World Survey of the Status of Anthropology," and the participants in the symposium were selected not merely as outstanding specialists but also for their ability to synthesize the views of others and for their broad grasp of anthropology in its totality. In planning for the symposium it was suggested that three broad categories be considered: (1) an inventory of modern anthropology, (2) an appraisal of modern anthropology, and (3) a handbook of world resources for research and education in anthropology. It was within this framework of categories that the symposium was conducted. The first and second volumes under review here are the published realizations of the first two categories. Though it is nowhere stated I presume that a third volume, dealing with the third category, will be forthcoming.<sup>1</sup>

*Anthropology Today: An Encyclopedic Inventory* contains the inventory papers, fifty in number, which were circulated among the participants before the symposium and later presented, though not read, and discussed at the symposium. This volume opens with a valuable preface by the indefatigable Director of the Wenner-Gren Foundation, Dr. Paul Fejos, in which he gives an interesting account of the history of the symposium. This is followed by an introduction from the pen of the doyen of American anthropologists, Dr. A. L. Kroeber, which extends the preface of

<sup>1</sup>This has now appeared: *International Directory of Anthropological Institutions*, Edited by William L. Thomas, Jr., and Anna M. Pikelis, Pages xii + 468, Published by the Wenner-Gren Foundation for Anthropological Research, Inc., New York; Distributed by the American Anthropological Association, Andover, Mass., 1953, \$12.50.—Ed.

Dr. Fejos. The second volume, *An Appraisal of Anthropology* contains the reports of the discussions of the inventory papers; it also contains an informative and charming preface by the editors, a very pleasant address of welcome by the founder, Dr. Axel L. Wenner-Gren, and an introduction by Dr. A. L. Kroeber explaining the mechanics of the symposium.

It should be clear that the appraisal volume must be read in conjunction with the inventory volume if the reader is to get anything out of the former—and there is a great deal, indeed, to be gotten out of the appraisal volume. Since the discussions in the appraisal volume follow the seven sections into which the inventory volume is divided the reader will want, every so often, to turn to the appraisal volume for the discussions. I shall confine myself in what follows to an account of the inventory volume and say here of the appraisal volume that it is quite as indispensable reading as the inventory volume, and should on no account be missed. In many ways it is the more readable and interesting of the two volumes.

The first paper, by Robert F. Heizer, "Long-range dating in archeology," presents an admirable survey of all the known methods of dating the remains of man. Kenneth B. Oakley's "Dating fossil human remains" gives an authoritative account of the fluorine method of dating human remains. In "The strategy of culture history" Irving Rouse discusses the various methods and approaches to the historical reconstruction of cultures. So much for "Methods" under the rubric "Problems of the historical approach."

Under "Results" William L. Straus, Jr. in "Primates" gives us a survey largely of what we don't know about the order of mammals to which man belongs. I found this a most disappointing paper. Surely, here was an opportunity to discuss not only what we do know but the results achieved by the particular methods used. "The idea of fossil man" by Pierre Teilhard de Chardin is not a particularly exciting piece, and Hans Weinert's "Der Fossil Mensch" contains so many errors of fact and so many misstatements, as Dr. W. L. Straus, Jr. points out in his discussion, it had been far better if it had been excluded from the volume. Erwin H. Ackerknecht's paper on "Paleopathology" is a brief and to the point survey of an important subject, while Carlos Monge's "Biological basis of human behavior" is a sadly mistitled paper, for what it deals with are physiological changes in men living at high altitudes. It will, nevertheless, interest those who are unfamiliar with Monge's book on "Trans-Andean Man." Henri Vallois' discussion of "Race" is readable but pedestrian. The next seven papers are masterly:

"Old World prehistory: Paleolithic" by Hallam L. Movius, Jr.; "Old World prehistory: Neolithic" by V. Gordon Childe; "New World culture history: South America," by Wendell F. Bennett; "New World culture history: Middle America," by Alfonso Caso; "New World culture history: Anglo-America," by Alex Krieger; "Historical linguistics and unwritten languages," by Joseph H. Greenberg; and "Style," by Meyer Schapiro.

Under "Theory" there is an excellent paper by Julian H. Steward on "Evolution and process" in social anthropology in which many good points are made, especially that one need not be a believer in unilinear evolution to accept the fact that there has been evolution in human societies. G. S. Carter's "The theory of evolution and the evolution of man" hardly lives up to its promise, for man is virtually completely omitted from Dr. Carter's discussion. J. G. D. Clark's paper "Archeological theories and interpretation: Old World," is excellent, as is Gordon R. Willey's "Archeological theories and interpretation: New World." Duncan Strong's "Historical approach in anthropology," is a most readable and scholarly paper, but it does not seem to me sufficiently critical of the lack of historical dimensionality which American anthropologists have on the whole exhibited.

Under the rubric "Problems of process" Floyd G. Lounsbury contributes a paper on "Field methods and techniques in linguistics" which will be found extremely helpful by field anthropologists with a minimum of training in linguistics, and it will also be found most interesting by the non-specialized reader. There is an excellent discussion of "Psychological techniques: Projective tests in field work" by Jules Henry and Melford E. Spiro and a most invaluable examination of "Interview techniques and field relationships" by Benjamin D. Paul; this latter piece will long form a breviary for all beginning field workers. Similarly invaluable is Oscar Lewis' discussion of "Controls and experiments in field work"; while George P. Murdock gives an interesting account of the work being done by the Human Relations Area Files at Yale in "The processing of anthropological materials." In this paper Murdock refers to most of the relevant work done by others, and thus provides a ready source for the relevant references. In "The contributions of genetics to anthropology," William C. Boyd puts the case for genetics as expertly as he always does, while Clyde Kluckhohn writes a fascinating chapter on "Universal categories of culture," which, as Forde points out, really deals with the determinants rather than with the categories of culture. Claude Lévi-Strauss on "Social structure" is altogether admirable,



while Harry Hoijer's "The relation of language to culture" should be read by everyone interested in the use and possible uses of language. "Structural linguistics" by André Martinet will be of interest only to linguistic students, but Stith Thompson's "Advances in folklore studies" will be of interest to everyone. It would be impossible to speak too highly of A. Irving Hallowell's "Culture, personality, and society": this is a masterpiece. Ralph Beals' "Acculturation" is an excellent historical account of the development of this new branch of anthropology, the study of culture changes when peoples of different cultures come into contact with one another. Margaret Mead's paper on "National character" is a fundamental piece which all workers in this field will have to read. "Cultural values" by F. C. S. Northrop is a valuable discussion of legal and cultural values, and David Bidney's "The concept of value in modern anthropology" is a stimulating paper, which is written from the viewpoint of a philosopher with a very scholarly background in anthropology. Of a totally different kind is Marston Bates' admirable paper on "Human ecology"; this is written from the viewpoint of the zoologist interested in man. "The strategy of physical anthropology" by S. L. Washburn is another stimulating paper by one of the most active of physical anthropologists. Robert Redfield's "Relations of anthropology to the social sciences and to the humanities," is an excellent and pivotal paper, which makes a bold and eloquent plea to anthropologists to re-survey themselves in the human situation.

"Problems of application" provides a well rounded discussion of the usefulness of physical measurements in non-traditional situations and for non-traditional purposes. "Growth and constitution" by J. M. Tanner presents an excellent survey, but omits reference to prenatal growth and constitution—a most important aspect of the subject, without the understanding of which postnatal growth and constitution cannot be properly understood. "Applied anthropology in medicine" by William Caudill provides an overall survey of the part that the applied anthropologist has been playing and can play in the future in medicine. Mary R. Haas' "The application of linguistics to language teaching" does what it says very clearly, and in "Applied anthropology in industry" Eliot D. Chapple gives a most interesting account of this important branch of anthropology. The next four papers, each written by an expert, are the best short surveys of their kind to be found anywhere of applied anthropology in government. Edward A. Kennard and Gordon McGregor deal with the United States, Daryll Forde deals with British Africa, G. Jan Held with the Netherlands, and Alfred Métraux with the United Nations.

In a final paper John Howland Rowe deals with "Technical aids in anthropology: a historical survey," which is not only very extensive in its survey but also very stimulating in its criticisms and suggestions. There is a list of contributors and an index.

So much for the formal annotation of the contents of the volume, a volume which will long constitute a landmark in the history of anthropology. This stocktaking of the present status of anthropology and the direction in which it is considered by these various authorities it should travel will constitute a fountain from which many will drink deep and heady draughts in the years to come. We all owe a very profound debt of gratitude to the Wenner-Gren Foundation for having made this stocktaking possible and for having made it available with such grace and expedition.

The organization of the symposium was a task presenting many difficulties; so far as was humanly possible that task seems to have been carried off consummately well. It is in no spirit of the carping critic therefore that I venture to make the following remarks. I hope they are not altogether the product of my own private prejudices.

Although anthropology as a scientific discipline is little more than half a century old its development, indeed, one might say its proliferation, has been rapid. The subject already has an extremely interesting history—it would have been pleasant to see that fact recognized at the symposium by the devotion of a separate inventory paper dealing with the history of anthropology.

It would also have been of great interest to have had an historical and analytic paper on the relations of anthropology to literature, to the novel, poetry, the drama, and criticism. One is led to believe that anthropology has had a much wider influence upon the modern world than even many anthropologists realize.

Finally, I should very much have liked to see a paper on the training of the anthropologist—surely, a unique opportunity was missed here.

It is possible that all these matters were considered by the planners of the symposium and for various reasons found impracticable of realization. Opportunities for the discussion of these matters will, no doubt, be afforded at some future time.

I must confess that while I found Professor Vallois' paper on "Race" good, it seemed to me rather heavily academic and not sufficiently concerned with the everyday realities of the situation. This is a besetting sin of many anthropologists who when they speak of "race" speak of it as if it were an abstraction, and too many of them, I am afraid, when

they speak of the Negro speak of him, too, as if he were an abstraction. Doubtless Professor Vallois was limited by his instructions, as I have said, his paper is good enough as far as it goes. What one misses is a presentation, in summary form of course, of the work which has been done in recent years in so many different fields relating to the problems of race prejudice, its genesis and development, and the various means which have been utilized to obviate or reduce its development. It seems to me that such an inventory paper and its discussion would have been most useful. During the last fifteen years we have made great progress in understanding the nature of race prejudice, and we have already had the opportunity to evaluate some of the methods of handling it. I refer to changing attitudes in the home, direct and indirect education, community measures, and legal ordinances, not to mention more general legislative measures.

It is interesting to recall here that not so long ago many pundits were asserting that "you can't legislate race prejudice out of existence." Well, astonishingly enough, we have seen legislative measures operating in the most substantive of ways not only to control the expression of race prejudice but also to reduce its virulence. And this, not merely by inhibition but by making it possible for people freely to mingle with one another where formerly they were enjoined by custom not to do so. The application of anthropological understanding to the solution of race problems might surely have found a legitimate place in the symposium. "Race" is one of the most pressing issues of the day, and the anthropologist, surely, has much to contribute towards the intelligent and effective meeting of that issue.

One thing becomes very obvious as one reads paper after paper as well as the discussions of these papers; namely, that anthropologists for the most part still lack an historical sense. Apart from Strong's paper there are scarcely any references to this important subject. Historical reconstruction as a method is more than ordinarily difficult when studying simpler cultures, but that is no reason why it should be treated as impracticable. Every culture is a product of a long history, and it should be the task of the anthropologist, among other things, to discover something of the nature of that history. The historical approach is most effectively realized by the archeologist, but this is an approach which is forced upon him, for archeology deals with cultures which are either extinct or no longer in existence in the form in which he recovers them. What we need is the application of the historical method to living cultures and not merely a broad overall approach to the history of

human culture as a whole. I regret to say that there seems to be little evidence that we shall get it. But enough of this.

Anthropology has come into its own. It now has to come into others. It has already made more than a beginning, as these two noble volumes most abundantly testify. No educational institution worthy the name of a college should be without its department of anthropology; nevertheless there are a number of major institutions without such a department, and numerous colleges are completely without any teaching in the subject. This is the more of an anachronism because anthropology should be the central core of education and therefore of the organization of the college curriculum. However, since this is scarcely recognized in those institutions in which a department of anthropology exists, it is perhaps a little too much to expect that a college education be built around a knowledge of anthropology.

Because anthropology is the science and art of humanity it stands in a pivotal position in relation to all other human knowledge. A truly liberal education should be first and foremost in humanity, and this no subject is better able to provide than anthropology. It is the subject about which and from which a truly integrated education could be developed, and it is my hope that this will some day be undertaken as a pilot study by some farseeing college administration. Meanwhile, the two volumes I have so inadequately discussed in this review should afford every stimulus to those engaged in the field of anthropology as well as to those who are interested in it to bring about this much to be desired change.

M. F. ASHLEY MONTAGU

## BOOKS RECEIVED

**STREPTOCOCCAL INFECTIONS.** Edited by Maclyn McCarty. x + 218 pp. Columbia University Press, New York, 1954. \$5.00.

**CONTRIBUTIONS TO THE ANTHROPOLOGY OF THE CAUCASUS.** By Henry Field. x + 154 pp. Papers of the Peabody Museum, Harvard University, Cambridge, Massachusetts, Vol. XLVIII, No. 1, 1953. \$6.50.

**CATALOGUE DES HOMMES FOSSILES.** Edited by Henri V. Valois and Hallam L. Movius, Jr., XIX Congrès Géologique International, Alger (1952), pp. 63-378, 1953.

**MUSIC THERAPY.** By Edward Podolsky. xii + 335 pp. Philosophical Library, New York. 1954. \$6.00.





EARNEST ALBERT HOOTON



## A DEDICATION

On May 1st, 1954, physical anthropology lost one of its most versatile and renowned leaders, Earnest Albert Hooton, Professor of Anthropology, Harvard University. It is with a deep feeling of appreciation that we who participated in this symposium join in dedicating the published version to his memory.

Dr. Hooton's position in the world of primatology was indeed a unique one for although his scientific writings cover a wide scale, he never contributed an original research paper dealing with a non-human primate. Yet his position was secure for he had with considerable success brought together and published in a popular, scientific manner much of the available information on "Man's Poor Relations." The publication of this book and the interest which he engendered in his students for non-human relatives have done much to establish primatology as a means of gaining perspective of the general problems of psychology, anthropology, and related sciences.

It was for these reasons that Dr. Hooton was requested to prepare the opening paper of this symposium. The other contributors were asked because of their special qualifications on some specific facet of the general topic. But the aim of the symposium was not only to bring together the palaeontology, comparative anatomy, anthropology, and psychology of the non-human primates but also to indicate how such knowledge can contribute to our understanding of the problems of human evolution. Such wide and, in a sense, nebulous aims would be foredoomed to utter failure unless the deeper and unifying aspects of the studies could be clearly and precisely stated. This was one of the final tasks which Dr. Hooton performed with his usual thoroughness: a thoroughness which gave the necessary coherence and meaning to the symposium as a whole.

Having witnessed the success with which Dr. Hooton handled his difficult role, the contributors dedicate this symposium to his honor. We hope that interest shown by the listening audience is indicative of a wider, growing interest in primatology which will remain as a lasting tribute to Dr. Hooton's efforts.

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## THE IMPORTANCE OF PRIMATE STUDIES IN ANTHROPOLOGY

BY EARNEST HOOTON

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ANTHROPOLOGY is the study of man, but difficulties have been encountered in formulating a satisfactory scientific definition of man. Huxley's "erect and featherless biped," apparently harks back to Plato, for Diogenes Laertius (*circa* A. D. 200) says: "Plato having defined man to be a two-legged animal without feathers, Diogenes plucked a cock and brought it into the Academy, and said, 'This is Plato's man.' On which account this addition was made to the definition—'with broad flat nails.'" As emended, this might include also the anthropoid apes. The most liberal definition of man with which I am familiar is that of Shaw, propounded in his introduction to "Back to Methuselah." He characterizes man as "only an amoeba with acquirements." This seems to me to be going a bit too far down the animal line, in addition to smacking of Lamarckianism.

The contention that we must settle upon a definition of man before

we can delimit the scope of anthropology is, however, something more than a semantic quibble. Efforts to separate man from other primates, by adding to Plato's qualifications for humanity other requisites, such as articulate speech, the possession of a soul, the development of a culture (whatever that is), etc., are too vague for usefulness and merely lead to further definitions, dialectics, and hair-splittings. Even the famous dictum that man is "the only animal that drinks when he isn't thirsty and makes love all the year round" does not rid us of the company of the great apes, nor even of the less socially acceptable monkeys.

There is, in point of fact, a rather serious disagreement as to the human or infra-human status of the erect, presumably featherless, biped Australopithecinae of South Africa, who almost certainly had feet modified away from the prehensile type for support in two-legged locomotion, who probably used sticks and stones with their emancipated fore-limbs, who satisfied the minimal and some further dental requirements for human status and yet seem to have had such small brains that their hats would not have slipped down over the ears of a chimpanzee. If these Australopithecinae were men, we shall have to enlarge the zoological scope of anthropology.

However, I do not really worry about the Australopithecinae—whether they were ape men or merely man apes—nor about any of these other taxonomic questions, which I have raised principally as the exhibition of that interest in terminology necessary to qualify myself as a social scientist. While the invention of a new term to describe old things might enhance the valuation of this preamble to a couple of days of papers on apes, monkeys, and their ilk, I shall fall back upon the use of the word "primatology." This term, although repellant and linguistically a hybrid, is redeemed if not legitimated by a dual connotation: the study of the highest animal order and the study which of all the -ologies is, or ought to be, *primus*, prime, or first in importance.

For it is my contention that Departments of Primatology should be established, not only as separate sections of our great research institutions, but also as teaching divisions in our universities. I shall endeavor to support this proposal, however, solely by pointing out how basic to the understanding of anthropology, sociology, psychology, and all of the other disciplines that pertain to man, is the investigation with every possible scientific technique and method of the primate animals grouped by Linnaeus and his successors in the order that includes man.

THE IMPORTANCE OF PRIMATE STUDIES TO PHYSICAL ANTHROPOLOGY  
AND TO GENERAL BIOLOGY*Taxonomy*

Taxonomy, which assigns man and all other animals to their proper pigeon-holes in the zoological filing cabinet, has become somewhat neglected in these days when anatomists prefer to be histologists and when zoologists are preoccupied with biochemistry, physiology, and endocrinology. Yet our weariness with the eternal wrangling over what constitutes a species, or a subspecies, must not blunt a keen realization of the continuing importance of researches in comparative anatomy and comparative physiology. The essay published by Edward Tyson in 1699, "Orang-Outang, sive Homo Sylvestris, or the Anatomy of a Pygmie compared with that of a Monkey, an Ape, and a Man," is one of the greatest achievements of science leading to an understanding of higher primate evolution. We cannot all be Tysons, but the rewarding task of comparing the apes and the more important monkeys with each other system by system is not merely incomplete; it has hardly been begun. In fact, there is not even one great anthropoid ape whose anatomy has been completely described, to say nothing of the intercomparisons with other genera.

*Human Evolution*

The foundations and the main structural features of the theory of human evolution are built up from the materials furnished by primatology. Apart from the general body of anatomical and physiological knowledge appertaining to all of *Homo sapiens* or modern man, which is utilizable as the human frame of reference in taxonomy and comparative anatomy, there is little, in fact almost nothing, in the anthropology of recent *Homo sapiens* that contributes substantially to the theory of man's evolution from other primate forms. There are no stages of human evolution discernible in the anatomy and physiology of recent man; only variations, mosaics of progressive and retrogressive characters, and a blurred picture of continuing differentiation, either without direction or possibly degenerative. We have to go back to the anatomically archaic forms of man, rather ponderously called palaeanthropic, before the accumulating evidence of an origin in apelike forms becomes plausible, and to the study of contemporary great apes and fossil apes before that evidence becomes impressive and conclusive.

The anatomist or anthropologist who attempts to reconstruct the skull

and the postcranial skeleton of a palaeanthropic type of man without a sound knowledge of the anatomy of the great apes and of at least the Old World monkeys is really only a sort of chiropractor operating in a situation where the patient cannot complain and the injury done to science, while not fatal, results in the mutilation of fact and the perversion of theory. Ignorance and naiveté do not excuse anyone for concocting hypothetical human ancestors from a few surviving bony fragments, with the help only of a couple of dissecting room skulls, a text-book of anatomy, and perhaps the cranium of one miserable chimpanzee. Piecing together the skeletal remains of *Homo sapiens* is not much more difficult than mending a pot, and missing parts may be restored with some confidence. But doing this job on, for example, the Australopithecinae requires a knowledge of infra-human primate anatomy possessed by few scientists in our time aside from Sir Arthur Keith and Adolph Schultz.

In figuring out the anatomical reconstruction and physiological interpretation of such post-cranial parts as the spine, the foot, and the pelvis, in forms so remote from modern man as are these South African ape men or man apes, a knowledge of human and anthropoid ape anatomy is insufficient. It has to be supplemented, as William Straus and other astute students know, by a thorough familiarity with the anatomy and the mechanics of posture and gait in terrestrial quadrupedal primates such as the baboon.

I need not labor this point further, but I cannot refrain from remarking that many persons who write eruditely and definitively upon the minutiae of dental morphology in ancient man and other animals, who do not hesitate to draw phylogenetic conclusions from a variation in form of the wrinkles separating molar cusps, and all that sort of stuff, overlook the fact that there does not exist as yet even an adequate, much less an exhaustive, description of the dentition of the common or garden chimpanzee, based upon any reasonably large series of specimens.

The range of variation of ape characters is extremely wide. In a Peabody Museum collection of some 300 chimpanzee crania from a restricted area in Liberia, this extensive variation manifests itself not only in dentition, but in cranial morphology and brain size. There are in this collection chimpanzees with sagittal crests, such as are supposed to occur only in male gorillas and male orang-utans. The cranial capacity varies so much that the uppermost limit overlaps the range of the gorilla. Ought we to build a towering structure of human phylogeny



upon the sands of ignorance of primate anatomy? We do not know enough about the anatomy and dentition of existing primates safely to interpret those of fossil primates, proto-human or infra-human. We sorely need dozens of trained investigators in the field so richly cultivated by Adolph Schultz; it is far too big and too important for even this great anthropologist to work alone.

### *Human Physiology and Pathology*

The science of physiology progresses largely by the use of experimental animals. The results of experiments upon and observations of the physiological processes of lower animals are utilized in human contexts. It seems reasonable to suppose that the closer the experimental animal is to man, structurally and physiologically, the more accurately will the experimental findings apply to man, whether in physiology or pathology. Among the most important physiological discoveries of the century, as respects its anthropological significance, and in the field of immunology, must be reckoned the antigens or blood substances, including the standard ABO blood groups, the MN, the Rh system, and others that are now too numerous to mention. The finding of blood substances among the great apes identical with, or closely similar to, those in man, made necessary a radical revision of theories of the date of origin and the prehistoric processes of diffusion of the human ABO blood groups and their genes. For example, it rendered untenable the theory that the New World was peopled from Asia before the mutations that originated the A and B substances (the p and q genes) merely because it was thought that all American Indians of unmixed blood belonged to group O. The accidental discovery of the Rh factor, derived from serological abuse of the humble rhesus monkey, has ramified into a complex system, which has great promise of significance in the determination of racial differences. Perhaps even more important is the discovery that the Rh factors and, by inference, many other blood properties are not, as previously supposed, biologically neutral or indifferent, but that, on the contrary, they may be vital factors in the selection for survival or extinction of the animal that possesses them. It seems probable that a much more extensive use of primate material not only in serological studies, but in the whole area of human physiology and biochemistry, might throw a brighter and clearer light upon human problems than is shed by depending upon one-candle experimental lower animals. It is realized that anthropoid apes are expensive, slow-breeding, and, in some cases almost impossible to raise in captivity, but these

obstacles would be surmounted if there were enough interest in their use for these purposes. That interest can be aroused only if the special value of infra-human primate physiology is recognized as bearing upon similar processes in human beings. Of course, monkeys and lower primates still are much cheaper to keep and much more rapid to reproduce, but, as far as I am aware, only the rhesus monkey is commonly used as a laboratory animal.

Some years ago Dr. S. Zuckerman, having reported a number of inter-generic and inter-specific crosses in the primate order that were recorded in the London Zoological Gardens, informed me in conversation of his desire and intention to carry on breeding and race-crossing experiments with lower primates, especially lemurs. Apparently this project never came to fruition. But *why* cannot genetic studies be made upon the lower primates? Must we forever depend upon genetic inferences carried over the vast chasm that yawns between man and the *drosophila*? Of course, rats, rabbits, and guinea pigs are zoologically more relevant to man than fruit flies, but do we not perhaps omit something very important when we fail to act upon the reasonable supposition that the genetics of the order to which we belong, even of the more remote genera and species of that order, are probably more closely applicable to our species than the genetics of lower mammals or of insects?

The study of human growth changes has been vitalized in recent decades by the use of x-ray methods and by physiological interpretations made possible by advances in endocrinology. In early days, the comparatively sterile studies of growth yielded little more than annual increments of anthropometric measurements and smoothed curves. The study of age changes from maturity to senility urgently demands the attention of medical and anthropological investigators, and not much has been done about it in the way of organized research. Both types of investigation, involving the development and maturation of the human organism and its gradual deterioration and disintegration, could be helped and accelerated, in my opinion, by the use of parallel studies upon infra-human primates—apes and monkeys. The latter could be subjected to experimental procedures that we hardly venture to try upon our own children or those of any other human parent. Such growth studies of the chimpanzee as have been carried out by Nissen, Gavan, and others in the Yerkes Laboratory at Orange Park have been, it seems to me, of enormous interest and value.

THE IMPORTANCE OF PRIMATE STUDIES TO CULTURAL ANTHROPOLOGY AND,  
IN GENERAL, TO THE UNDERSTANDING OF HUMAN BEHAVIOR

Man's use of tools and weapons has usually been considered as one of his prime distinguishing characteristics, and so it is. However, the manual equipment of the infra-human primates is, in some genera and species, only a little inferior to that of man. All of you are familiar with the contributions of Koehler, Yerkes, and other students of primate psychology to the use of tools by chimpanzees and other infra-human primates. These studies have great significance with reference to the beginning of tool-using in our early human and proto-human ancestors. But more intensive investigations of tool- and weapon-using in apes and monkeys are needed and it would seem that the relationship of brain and general neurological development to the tool-using capacity might be studied with profit.

The ever-intriguing *Australopithecinae* had possibly arrived at an evolutionary status in which they were using tools of the ready-made kind and were perhaps even attempting to alter natural objects the better to serve such purposes. How large a brain, or how complicated a nervous organization, is required to effect the transition between using natural objects and fabricating or trying to make tools and weapons? We need the primatologist in trying to solve this problem.

Social anthropology and sociology have been so greatly enriched by studies of the family life and social habits of infra-human primates, notably those of Yerkes, C. R. Carpenter, S. Zuckerman, and Henry Nissen, that it seems superfluous to comment in any detail upon them. I shall no doubt evoke the indignant disagreement of social anthropologists when I suggest that more is to be learned about the genesis of the human family and the beginning of social organization and community life in early man by the study of contemporary infra-human primates living under natural conditions than by the studies of retarded human groups living today under conditions variously described as "primitive," "uncivilized" or "savage." In my time I have read a fair number of excellent anthropological monographs dealing with these modern "primitives" or "pre-literates"—all the way from the Negrito, the Bushman, and the Australian upward to higher levels of material culture and social organization (if one may be permitted to imply that there are different levels). Far be it from me to impugn the value of these studies, but these contemporary savages are not "primitive," not on the evolutionary

upgrade, not the stuff of which societal progress is made. Whether environmentally underprivileged or genetically underendowed, or both, they are cultural imbeciles or morons—at any rate if we believe our “civilizations” are superior to their rude ways of life. If they are too smart to “fall for” our higher cultures, they are that much further from our ancestral prototypes.

To me, what Carpenter tells us about the family life of the gibbon, and the contrasts between the group and individual life of, first, the *Hamadryas* baboon, then the macaque, and then the howling monkey, are far more instructive for the history of the prehuman, proto-human and early human social groupings than any of the stuff on present-day savages written by anthropologists.

Of course these splendid pioneer studies of the behavior of infra-human primates in the wild have already been incorporated into the basic literature of anthropology. But I view with utmost dismay the lack of sustained interest in such studies, the present reluctance of institutions to promote them, and the difficulty of financing them, which I assume to be the reason for their discontinuance by Carpenter and for the failure of other younger men to take them up where he has left off. I know of no studies bearing upon man's cultural and social origins that have been begun so brilliantly, that have progressed so magnificently, and that have been abandoned so miserably and ignominiously. It is as if one were to dig for oil, strike a gusher, and then immediately cap it up and go away and forget about it. Anthropology needs more studies of primate sociology.

### *Personality, Temperament, and Intelligence*

The studies of primate intelligence, personality, and temperament so painstakingly and successfully conducted by experimental animal psychologists in the past 30 years and more are just as interesting and important to the anthropologists as to any psychologist. It will be a serious detriment to the development of anthropology if the interests of psychologists in this field of investigation flag or lapse, as I sometimes fear to be the case. It may be pointed out that of the anthropoid apes, only the chimpanzee has received any considerable amount of attention in this respect. I do not, of course, forget the splendid studies of Yerkes on *Julius the Orang* and on the young female gorilla, *Congo*. Other isolated studies might be mentioned, all invaluable to the student who feels that a knowledge of the psychology of the primates is necessary

for the interpretation of human mental development. It should be clear that everything known to us about individual morphological variation in the higher primates, especially the great apes, leads to the surmise that they must differ individually so widely in temperament, in intelligence, and in personality that many studies of single subject apes will be required to establish the ranges and the norms. Probably newer and better techniques of studying the individuality of apes and monkeys will bring us even more valuable insights into the interrelationship of body and mind within the same species.

I presume that the specialties of linguistics, phonetics, neurology and neuro-anatomy have developed a long way since primate investigators first tackled the problem of the capacities of the great apes for articulate speech. The subject urgently requires further study and experimentation.

### *Conclusion*

Recent man and his fossil precursors may be taken to represent the apex and the uppermost courses of a primate pyramid, the bottom of which was laid down in the Eocene, a matter of 60 millions of years ago. Some existing forms represent survivors from all or nearly all of the successive courses topped by man. There are many fragmentary blocks in each of these courses and some are missing entirely. These are the extinct primate forms, a few preserved in part as fossils. Every system of the human organism—skeletal, muscular, circulatory, digestive, nervous or what not—is built upon its precursors in the underlying layers. Every detail of each system and every variation has originated in one or other of the lower courses. If we are to understand man, if we are to be anthropologists in a real sense of the term, our knowledge of every aspect of the human organism and its functioning should extend downward to its lower primate origin. We can leave the earlier precursors of our order to the general zoologists and to the palaeontologists.

If anthropology is going to amount to anything as a complete science of man, it will have to avoid splitting itself up into specialties that tend to secede and join up with other disciplines—such as social anthropology going over to sociology and social psychology, physical anthropology to human anatomy and general biology, archaeology to fine arts and history. These fissions and new agglutinations result principally in dismembering man and his behavior, pushing Humpty Dumpty off the wall, so that nowhere is there to be found a comprehensive treatment of the total human animal. The way of salvation for anthropology lies in main-



taining its unity, even though the title is pretentious and overambitious for the present coverage by a few practitioners. But under this all-inclusive name anthropologists can welcome to their hospitable board all sorts of other scientists, who may not only sit with them and put their feet under the anthropological table, but are also privileged to bring with them their own provender, of which the sponsoring anthropologists gladly and greedily partake. So in this symposium on primate studies, sponsored by anthropology, the contributors are psychologists, palaeontologists, geologists, dental specialists, human anatomists, comparative anatomists, serologists, and one or two anthropologists. We appreciate what our colleagues bring to us and they can find perhaps a warmer reception here for their primate studies than in their own specialties. We do not proselytize; we do not want to seduce them away from their own disciplines, but we insist upon regarding them as true, full-fledged anthropologists. Paraphrasing some Roman or other we anthropologists say: *Primatus sum, nihil primatum mihi alienum puto*, which, being translated, is "I am a primate; nothing about primates is outside of my bailiwick."





## FOSSIL PRIMATES IN THE NEW WORLD (ABSTRACT)

BY G. L. JEPSEN

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ONLY three orders of living mammals, the marsupials, insectivores, and carnivores, have longer geological histories than the primates whose oldest known members occur in North America in sediments of mid Paleocene age,—about 65 million years ago. These earliest prosimians, mostly tree-living fruit-eaters, are distributed among five families and present many intricate problems of origin and distribution. Their relationships among themselves and to the living prosimians of the Old World and to the anthropoids of both hemispheres are obscure.

Two of these early families, the Carpolestidae and the Phenacolemuridae were exclusively North American in distribution and became extinct in the early Eocene. A third family, the Plesiadapidae, has a similar range in North America but it survived a little longer in Europe, after appearing there in the late Paleocene. Members of the other two families, the highly specialized Apatemyidae and the tarsiiform Anaptomorphidae lived continuously in North America, for a period of about 30 million years, until early Oligocene time. They also inhabited Europe during the Eocene, and, in this epoch a sixth prosimian family, the Adapidae, appeared in both North America and Europe.

There is no record of primates in North America from the early Oligocene to the time of human occupation, a gap of approximately 35 million years. However, in South America a few fossil platyrrhine monkeys of Miocene age have been found in Patagonia and Colombia, and an extinct genus, Pleistocene or recent in age, from Jamaica brings a record of fossil anthropoids closer to North America. All these forms (the total is only a few fragments representing three or four genera)

were apparently closely related to the living ceboids and marmosets, and do not indicate their relationships to the earlier North American groups or to Old World primates. The platyrrhines were probably derived, however, from some part of the North American early Tertiary prosimian stock that reached South America by land in the Paleocene or by raft somewhat later.

A few more than 100 genera of extinct primates are now known. Most of these, about 70, are prosimians (tupaoids, lemuroids, and tarsoids) which are represented by a few more genera in the New World than in the Eastern Hemisphere. Only one genus, an early Tertiary form, occurred on both sides of the Atlantic.

The distribution pattern of the genera of prosimians in North America and Europe suggests some interesting speculations. In North America the number of genera of primates increased rapidly from the earliest appearance in the mid Paleocene to the greatest figure, 13, in the early Eocene, and then declined. In Europe the rise to the same maximum number of genera was a little later and the disappearance occurred even faster.

Evidence from fossil plants of a temperature increase in North America between early Paleocene and late Eocene time might be correlated with the increase of the prosimians, and their decline may have been the result of selective competition in the great evolutionary surge of the rodents, which had earlier overcome the multituberculates, in mid and late Eocene time.





## THE GEOLOGIC HISTORY OF NON-HOMINID PRIMATES IN THE OLD WORLD

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DISAGREEMENTS among students of the primates are many and profound—a statement that hardly possesses the charm of novelty. Since these disagreements extend to what should and what should not be included in the order both at the bottom and, in the family Homi-nidae, at the top, it becomes necessary at the outset to define the term “non-hominid primate.” In this discussion, it will include the tupaoids and exclude the *Australopithecus* group. As thus limited, the topic is a very large one, requiring for thorough treatment far more space than can be allotted here. In an attempt to cover as much ground as possible, the setting in which Old World primate history unfolded will be touched upon, the nature of the fossil record reviewed, some points in it singled out for mention, and, in conclusion, a brief discussion given of certain theoretical interpretations that seem reasonable in the light of the knowledge now available.

### THE SETTING

The evolution of the primates in the Old World took place over the greater part of Eurasia and Africa. We may confidently infer that this immense area has always been diverse climatically and topographically, although not as much so, as regards climate at least, in the earlier Tertiary as during the latest Tertiary, Pleistocene, and Recent periods. It was, however, much more cut up at various times in the past than it is now. A great negative belt in the earth's crust extended across it from the Atlantic to the Pacific. This was the site of the Tethys Sea, of which the Mediterranean is a remnant, a major barrier during much

of the Tertiary to free faunal interchange between Europe and Northern Asia, on the one side, and Africa and Southern Asia, on the other. This barrier, of course, was neither complete nor continuous; the constant inflow of sediment combined with temporary cessation or slowing of subsidence here and there would have resulted in temporary land connections or insular stepping stones at various places along its enormous length. There were other negative belts, small only in comparison with the Tethys, that played their parts in the fragmentation process; to name only one, I may mention the Uralian trough, which occupied roughly the present site of the Ural mountains and served for some time as a partial barrier to east-west faunal movements in the northern mass. In addition to the long continuing, although not continuous, barriers presented by the negative belts, parts of the land areas were at times flooded by shallow epicontinental seas that must effectively have isolated areas of higher ground. Western Europe, for example, must have been an archipelago several times in its history. Concurrently with these ever-changing relations between land and sea, climatic fluctuations certainly took place, together with concomitant changes in the distribution of forest and savannah, steppe and arid region. Under such conditions, ranges would be shifted, contracted, or expanded; contiguous regions would be sundered, perhaps fragmented, to remain separated for longer or shorter periods of time and then to be reunited. This would seem to be true especially for the earlier part of the Tertiary. As time went on, the area became progressively more unified. Conditions, in short, were excellent for evolutionary diversification. With Old World primate evolution occurring in a setting such as this, it is difficult to take seriously the pronouncements so frequent in the literature that this or that group of primates arose in this or that region—certainly not in the present very sketchy state of our knowledge.

#### THE NATURE OF THE RECORD

Just how sketchy this knowledge is, a glance at the map (fig. 1) reveals. The various symbols show, very roughly, the distribution of fossil primate finds in space and time. They designate regions rather than specific localities and it was unfortunately not possible on this scale to indicate what part of an epoch the symbols represent. A jibe frequently leveled at distribution maps is that what they really show is the distribution of collectors, not that of organisms. The charge must be fully admitted in this instance. Only in Western Europe, the region





FIG. 1. OCCURRENCES OF NON-HOMINID FOSSIL PRIMATES IN THE OLD WORLD.

longest and most intensively worked, do we have anything that even remotely approaches a continuous record. The scarcity of records from the other, much larger, regions stands out in striking contrast. Europe contains the only Paleocene locality that has yielded primates, and there also is found the only Eocene sequence. Extra-European Eocene localities number but two, both Late: one in northern China and one in Burma. All we know about primate life in the Oligocene is derived from a few finds in Egypt and Central Asia. Were it not for the East African Miocene, our records for this epoch would be meager indeed. The Pliocene is represented by relatively abundant although fragmentary material from India; elsewhere chiefly by various finds in Europe, including one new one of outstanding importance—the new material of *Pliopithecus*. Pleistocene symbols are more numerous than any others on the map, but this is unfortunately no indication that our knowledge of the primates of this epoch is adequate. The fact is that nearly everywhere, Western Europe excepted, the surface has barely been scratched.

Going on a consideration of the number of genera known (table 1), the deficiencies of our knowledge become even more apparent. There are 43 genera of living Old World non-hominid primates, give or take a few in either direction, according to taste in lumping or splitting. About 60 extinct genera are known, approximately half again as many as the living. This small total becomes even less impressive when we reflect that the vast majority are known only from fragments of mandibles and maxillaries. The number of forms of which we have a fair knowledge of skull structure and/or some acquaintance with the postcranial skeleton is far fewer. The roll of these is soon called. Paleocene: *Plesiadapis* (from North American material); Eocene: *Adapis*, *Pronycticebus*, *Necrolemur*; Miocene: *Progalago*, *Limnopithecus*, *Proconsul*; Pliocene: *Mesopithecus*, *Liopyithecus*, *Pliopithecus*; Pleistocene: most of the Malagasy lemuroids and the African cercopithecids, the Chinese material of *Rhinopithecus*. For the Tertiary this makes a total of 10. Paleontology can speak with some authority on the taxonomy and phylogeny of certain of the living orders of mammals—for example, in Artiodactyla extinct genera outnumber living by nearly 4 to 1, in Perissodactyla by 25 to 1; it is evident, however, that it cannot yet do so for the Primates.

At this point, perhaps, the reader might reasonably expect the discussion to be concluded for lack of evidence. Things are not quite as bad as that, though. In any survey of a history it is very proper to

TABLE 1  
Geological Record of Non-Hominid Primates in the Old World

Divisions of Cenozoic Time and their estimated durations	PROSIMIANS										CATARRHINES								Genera Known in the Divisions of Cenozoic Time		
	Tupaioids		Lemuroids				Lorisoids		Tarsioids		Inc. Sed.	Cercopithecoids		Inc. Sed.	Hominooids						
	Anagalidae	Tupaidae	Plesiadapidae	Adapidae	Lemuridae	Indridae	Daubentonidae	Lorisidae		Microchoeridae	Anaptomorphidae	Tarsiidae	Aptemnyidae	Prosimiidae	Cercopithecoide	Cercopithecoide	Inc. Sed.	Dryopithecinae		Hypobathinae	Ponginae
								Lorinae	Galaxinae												
Recent	..	5	..	..	6	3	1	4	2	..	..	1	..	..	10	6	..	..	2	3	43
Pleistocene L	..	..	..	..	6	6	..	..	..	..	..	..	..	..	1	1	14	..	1	1	14
1 million E	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	1	11	..	1	1	6
Pliocene L	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	1	..	2	1	1	1
11 million E	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	1	..	1	..	..	1
Miocene L	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	3
16 million E	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..	1	..	..	3
Oligocene L	1*	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	2	..	6
10 million E	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1*	..	..	0
Eocene L	..	?	1	1	3	..	..	..	..	2	1	1	1	2(1*)	..	..	2	..	..	..	11
20 million E	..	..	1	1	4	..	..	..	..	1	1	..	..	5	..	..	..	..	..	..	13
Paleocene L	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	4
17 million E	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2
Genera	2	5	4	4	10	6	1	5	3	3	2	1	2	7	16	8	6	1	9	3	103
Total	0	5	0	0	6	3	1	4	2	0	0	1	0	0	10	6	0	0	0	3	43
Living	2	0	4	4	4	3	0	1	1	3	2	0	2	7	6	2	6	1	9	0	60
Extinct	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

\* Exact horizon doubtful.  
? Systematic position uncertain.  
N. B. A number of genera extend over more than one division of time.

state what the gaps are and where they occur, but it is equally proper to go on and do as well as possible with what is in hand. Every primate fossil is a precious relic that contributes its bit to the history of the order. True, the evidence thus far contributed is often capable of conflicting interpretations, but sooner or later matters iron out; new discoveries permit new perspectives, and progress, however halting, is made. Paleontology may not as yet be able to speak with authority, but it is now in a position to make suggestions that seem reasonable and worthy of attention. From here on, then, we can begin to look more at the positive, or brighter, side.

#### DISTRIBUTION

Some interesting data concerning geographical distribution are available. The scanty Pleistocene records show that the orang utan was in India during the Early Pleistocene, and thus suggest that it was present in south-eastern Asia throughout most if not all of the epoch. The few remains of Pleistocene gibbons extend the present range of *Hylobates* into southwestern China. Interglacial climates more favorable than the present permitted *Presbytis* to range westward into Europe and *Macaca* to extend as far north as England. *Papio*, together with *Macaca*, has been reported from the Mid Pliocene of India, but more complete remains would perhaps make a new generic assignment necessary. It is clear that, during the later Tertiary, the gibbon group ranged widely over the Old World, together with the rather heterogeneous and probably artificial assemblage known as the Dryopithecinae. The very few later Tertiary and the Pleistocene records of prosimians are all within the areas now occupied by their surviving relatives, a fact which supports the inference, reasonable on general grounds, that the Prosimii had by then been displaced by the catarrhine expansion, and relegated to the marginal areas or ecologic niches they now occupy. Our knowledge of earlier Tertiary prosimians is almost wholly limited to Western Europe, but we can be sure that the group was very wide spread in the Paleocene and Eocene. In general, as Cenozoic time went on, and Eurasia and Africa became progressively more unified, increasing opportunity for wide dispersal was available to successful groups.

The most important single zoogeographical datum in connection with primate history is this: since the Early Eocene, Old World and New World primate evolution appear to have gone their separate ways. We can state with confidence that some Paleocene primate exchange took

place between the hemispheres, witness the common presence of plesiadapids. *Plesiadapis* itself, by the way, is the only genus, other than *Homo*, known to occur in both. The lack of Early Eocene genera common to the two is surprising, because this was the time of greatest faunal interchange between Eurasia and North America, indicating a broadly open migration route (Simpson, '47). Primates surely participated in this interchange, but perhaps ecological barriers may have prevented their rapid spread westward in the Old World. The Early Eocene primate fauna of eastern Asia, if and when it is made known, may well turn out to be more similar to that of North America. So long as nothing is known east of Europe for this part of the Tertiary, it is of little use to speculate concerning the absence of various American super-generic groups in Europe. Suffice it to say that the general cast of the primate fauna, the degrees of evolutionary advance, etc., were broadly comparable in the two areas.

Following the Early Eocene connection, Eurasia and North America were apparently separated until the Late Eocene. Neither during this nor any of the later connections is there evidence of any primate migrations until *Homo sapiens* arrives on the scene. Conditions in the vicinity of the bridge, which was very probably in the Bering Strait region, were evidently unfavorable climatically for members of the order in existence at the various times of connection. This very early separation of the basal primate stock has a decided bearing on major taxonomy, as will appear.

#### SOME ASPECTS OF THE RECORD

Space is lacking for any detailed review of the factual evidence, and since nearly all of it has been so well described by authors whose works are thoroughly familiar, this is not too serious. I shall therefore take up only a few specific points and touch on one or two matters of general interest. The absence of any definite records of the Tupaiidae is puzzling, because, be they primates or only near-primates, they have certainly come down to us from the earliest times. It may perhaps be that we have them and do not know it. The tupaiid dentition is quite characteristic, but it is possible that this might have been acquired in post-Eocene time, with Eocene and Paleocene representatives consequently remaining undetected. The question mark in the Mid Eocene in table 1 refers to two genera recently referred to the family by Weitzel ('49). Unfortunately, his descriptions are cursory and given in general



terms, and he does not figure the tooth crowns. The general body form is quite tupaiid-like, but this by itself is hardly sufficient evidence. These forms may perhaps be related to the Paleocene adapisoricids and these in turn could conceivably be tupaoids, but this is all very conjectural.<sup>1</sup> The tupaoid affinities of the Anagalidae have recently been called in question. Bohlin ('51) has described *Anagalopsis* from a deposit in Central Asia that is not precisely dateable, but which may fall somewhere in the later Oligocene if we may judge from the dentition of this form, which is more advanced than that of *Anagale*. Advanced in a peculiar way, the teeth being sub-hypsodont and unilaterally so, in the manner of many rodents and some other forms. This is a decidedly odd feature for a primate, although not in itself grounds for excluding the family from the order. Bohlin regards the structure of the bulla, as he interprets it, as the decisive character. Since this has an open U-shaped cleft beneath the porus proper, and no meatus, he concludes that it must be formed by the tympanic, and not by the entotympanic as it is in tupaoids. It seems to me, however, that an entotympanic in the course of phylogeny might assume such a form, and I am therefore not yet prepared to throw overboard Simpson's careful evaluation of the evidence favoring inclusion of the anagalids in the tupaoids.

The whole Early Tertiary prosimian complex bristles with difficulties. Forms and series of forms are shuttled about from one division to another and there is disagreement over what should be included and excluded. For example, the microchoerids are placed by Gregory, Le Gros Clark, and Simpson in the Tarsioidea (by the last as a subfamily, Necrolemurinae, of Anaptomorphidae), while Hürzeler ('48), who has recently completed a careful study of them, believes that they are closer to the lemuroids and entitled to rank as a distinct superfamily. For some, the Apatemyidae are primates, for others not, and so on. Such disagreements among highly competent authorities, the conflicting evidence responsible for them, and the number of genera that cannot be definitely assigned, strongly suggest that the distinction between lemuroids and tarsioids was not at that time very profound (Simpson, '45; Barth, '50).

The mosaic of characters that makes classification of these forms so

<sup>1</sup> Following Teilhard de Chardin, the adapisoricids have been placed in the insectivore family Leptictidae by most authors. The early Eocene species referred to *Adapisorex* by Teilhard is a leptictid, but the type and other late Paleocene species do not appear to be referable to this family.

difficult may be traceable to conditions prevailing in the area during the early Tertiary. The reader will recall the changing relations between land and sea, the fluctuating climates, and the shifting vegetation zones that the geologic evidence seems to indicate. Note that the Paleocene and Eocene together make up almost exactly half of Tertiary time, if we can trust the present crude estimates of the duration of the epochs. Under such conditions and over such a length of time, small scale adaptive radiations would tend to arise in various separated regions. Reunion of these regions would lead to intergroup competition and to the reduction or elimination of the less well adapted of those groups that had happened to evolve in similar directions. Renewed separation would start the process anew. The genetic complex of any of these various stocks must have had much in common with those of all the others. Many mutations acting in these substrates would thus tend to have similar effects in distinct stocks, the closer the more nearly parallel the trends under way. As a result, not only would similar details of dental morphology be attained, but independently achieved characters would occur in the skull and post-cranial skeleton as well. The net result would be a confusing array of small groups, each one resembling the others in a variety of ways, a situation extremely difficult to deal with on the basis of fragmentary fossil material. A small sample from one region, such as we have from Western Europe or from Western North America, obviously will not permit us to reconstruct very much of the story. In fact, if paleontology succeeds in even partially unravelling the tangle it will be doing very well indeed.

At the end of the Eocene and the beginning of the Oligocene there appears a small array of genera—such as *Amphipithecus*, *Moeripithecus*, *Parapithecus*, *Propliopithecus*, "*Kansupithecus*"<sup>2</sup>—that was probably of the greatest importance in primate history. It is more likely than not that these forms arose from some anaptomorphid stock, and very possible that they, or rather the group they represent, were broadly ancestral to the Hominoidea and to the Cercopithecoidea. It is therefore the more unfortunate that our knowledge of them is confined to the lower jaw. One, *Propliopithecus*, has been hailed as an ancestral gibbon; it might about equally well, perhaps, be regarded as standing somewhere in the line of the Hominoidea as a whole (the others occur in the table under *Catarrhini incertae sedis*). It is at this point in history, just

<sup>2</sup> This name is technically invalid, Bohlin ('46) having failed to name a species.

when things are getting really exciting, that the curtain descends on the higher primates, to remain down for two full subepochs. When it rises again in the Early Miocene, we are presented, thanks to the magnificent discoveries in East Africa, with an undoubted cercopithecoid, generalized pongids and a primitive gibbon.

Taking up the Cercopithecidae first, what strikes the eye is that the colobines have, in the books at least, a longer recorded history than the cercopithecines. This is based on *Mesopithecus*, known from the Early Pliocene, to which the Early Miocene East African form has been tentatively referred in preliminary notices. There is something a little puzzling here. The living colobines tend to be rather strictly arboreal, and their diet, as is well known, consists largely of leaves, for the digestion of which they have a specialized stomach. *Mesopithecus* is probably the most completely known fossil primate and its remains are quite common in Pontian deposits, skulls having been found in groups (Abel '27, p. 133). The associated fauna is that of a steppe region, horses, antelopes and other open country forms occurring in numbers. If *Mesopithecus* was a colobine with the diet and habitat preferences of its living relatives, why is it so common in a steppe fauna? A form living in trees along watercourses, as *Colobus* does in East Africa today, would hardly leave skulls in groups. A reexamination of the affinities of *Mesopithecus* would seem in order; the field evidence suggests cercopithecine relationships. The remaining cercopithecoids call for no comment in a review of this brevity.

The case of *Oreopithecus*, frequently considered to be a cercopithecoid, deserves passing mention, if only as a horrible example of what should not happen. Originally described in the 1870's, a literature of approximately 80 papers has grown up around it. Three views as to affinities have been held: that it was a pongid, an aberrant cercopithecoid, or a sort of connecting link between the two. Hürzeler ('49) has recently made a thorough restudy of the genus and has concluded that it is a pongid ("anthropomorph") of uncertain affinities, and has nothing to do with the Cercopithecidae. It is shown in the table in the Early Pliocene under Pongidae *incertae sedis*. Now comes the depressing part of the story. Hürzeler believes that only 11 of the many papers describing or referring to the animal were written by authors who had seen original material. The others were based on the previous literature, on the published figures, or on some casts that appear to have been widely distributed. The figures were inaccurate and the casts were

misleading. Schwalbe, author of the longest and most quoted paper, apparently worked from the casts. Gregory, also working from the casts and laboring under the misapprehension that the age was Early Miocene, thought he detected a resemblance between *Oreopithecus* and the problematical *Apidium*, and from this stems the view that *Apidium* might have had something to do with the ancestry of the cercopithecids. Students of the fossil hominids must all be familiar with situations of this sort, expenditures of time and energy that resulted only in confusing the issue. This and similar cases should inspire us to take steps to insure that such does not occur again. Of this more anon.

On dental evidence, the gibbons can be traced back to the Early Miocene, certainly, and perhaps on back to *Propliopithecus*. Of the Ponginae, neither *Pan* nor *Gorilla* has a fossil record. *Pongo* is recorded from teeth throughout the Pleistocene, and Hooijer ('51) has recently discussed a Mid Pliocene  $P_3$  from the Siwaliks, which he finds indistinguishable from that of the living species. The bulk of the pongid records is of course formed by the Dryopithecinae. The relatively numerous Late Miocene and Pliocene finds are unfortunately not very helpful in tracing lines of descent, but they do show that a fairly rich variety of hominids was then in existence. The magnificent finds of *Proconsul* are so familiar that there is no need to go into any detail here. It is enough to say they reveal that an Early Miocene pongid had a brain of generalized catarrhine type, a jaw that had relatively narrow incisors and lacked a simian shelf, and limb bones that were not specialized for brachiation. Presumably it progressed to a considerable extent on all fours. The contemporary gibbon *Limnopithecus*, the Pliocene gibbon *Pliopithecus* (Zapfe, '52), and such few skeletal fragments of later dryopithecines as we have, combine to suggest that a similar body form, at least, was characteristic of Miocene and earlier Pliocene pongids generally.

#### SOME POSSIBLE INTERPRETATIONS

So much for this very brief and necessarily incomplete survey of the available facts. A body of data requires organization if it is to have meaning, and paleontological data are perhaps most succinctly expressed in the form of phylogenetic diagrams. The fact that such diagrams are notorious for the wide difference of opinion they usually display does not detract from their usefulness as shorthand expressions of different viewpoints. The scheme shown in figure 2 was published

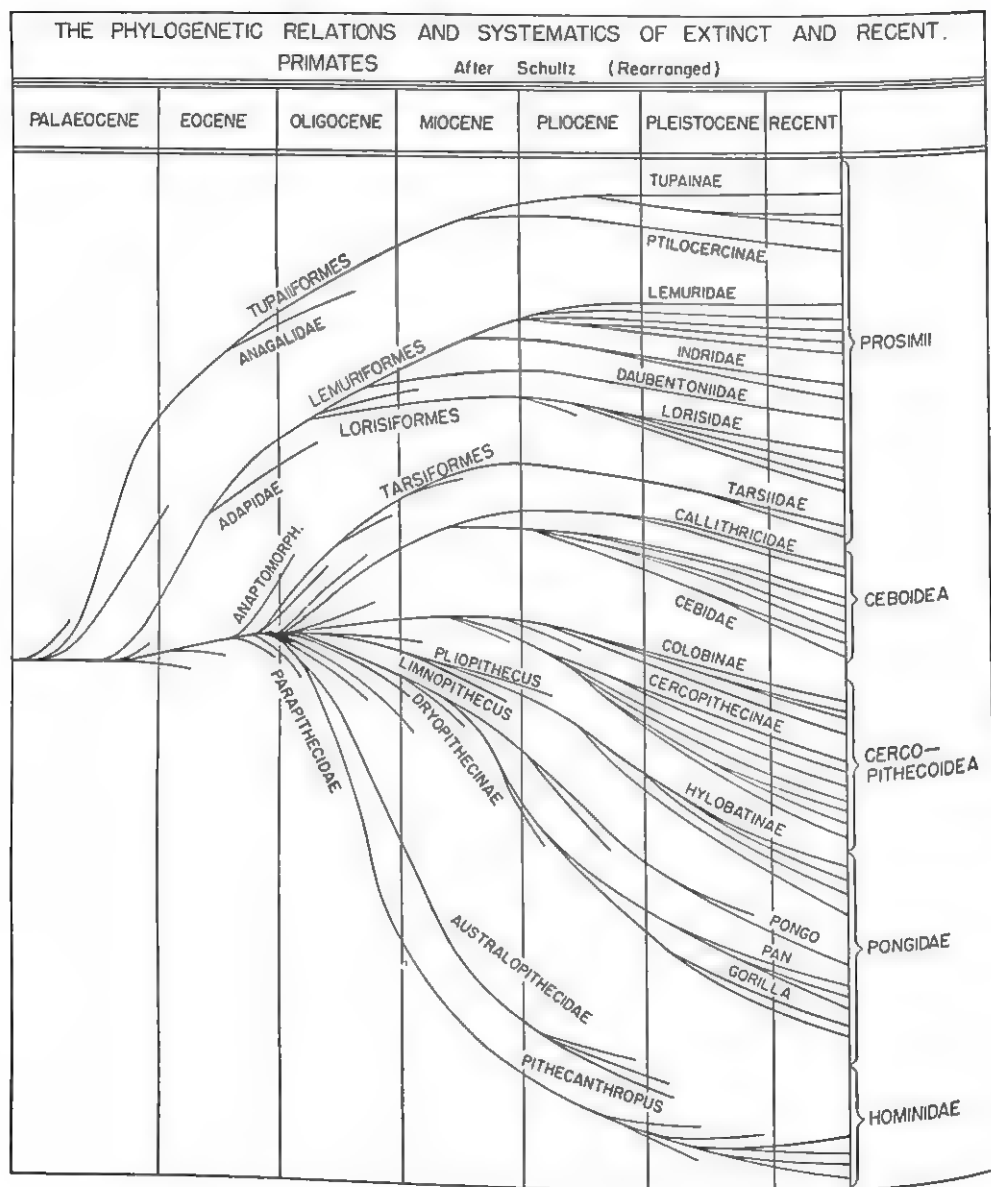


FIG. 2. ONE VIEW OF PRIMATE PHYLOGENY. AFTER SCHULTZ, REARRANGED.



recently by Adolph H. Schultz ('53), one of the great students of Recent primates. It contains some questionable features. To begin with, some of the lines appear to be split unnecessarily far back. I find it incredible that the Homiidae should have originated at the beginning of the Oligocene, or that the *Australopithecus* group should have parted company with them shortly thereafter. The *Pan* and *Gorilla* lines surely were not separate in the Early Pliocene, and it is perhaps doubtful if the *Pan-Gorilla* and *Pongo* phyla go back as far as the Mid Miocene. On the other hand, the break-up of the Cebidae certainly took place long before the Pliocene. Going on to more general topics, it is misleading to represent all extinct groups as so many minor twigs from main branches that extend without deviation or interruption from the distant past to the present, and the depiction of a main trunk running from Paleocene almost to Oligocene is somewhat of an oversimplification. Schultz's diagram has not been singled out merely for the sake of capricious criticism, but because I suspect that it is a rather representative example of how primate evolution may appear to those who look into time from the vantage point of the Recent.

Figure 3 is submitted as an example of how the picture appears to one who tends to look into time from the opposite direction.<sup>3</sup> Viewed in this light, primate history has the appearance of a succession of radiations of varying scope.

The dashed lines at the base of the figure are not there for purely decorative purposes. As Professor Jepsen remarked in the course of the Symposium, only three living orders, one of them non-placental, have a longer recorded history than the primates. A character fundamental to the evolution of the Theria was the acquisition of the so-called tribosphenic molar, from which the primate and all other types have been derived. It is now known that this molar type had come into existence by the middle of the Cretaceous Period. During that part of the Age of Reptiles represented by the Late Cretaceous—a long stretch of time, probably longer than the Eocene, for example—mammals must have undergone a considerable amount of diversification. At present,

<sup>3</sup> Those familiar with the scheme presented by Simpson in his *The Meaning of Evolution* ('49, fig. 17, p. 91) will note a considerable degree of resemblance. The two are actually independent. The explanation for this lies in the fact that Simpson's book exists in two editions. In one, which I read, presentation and discussion of factual evidence is abbreviated, and the figure in question is not included. I did not see it in the first edition until after figure 3 had been drafted. The agreement between the two is encouraging.

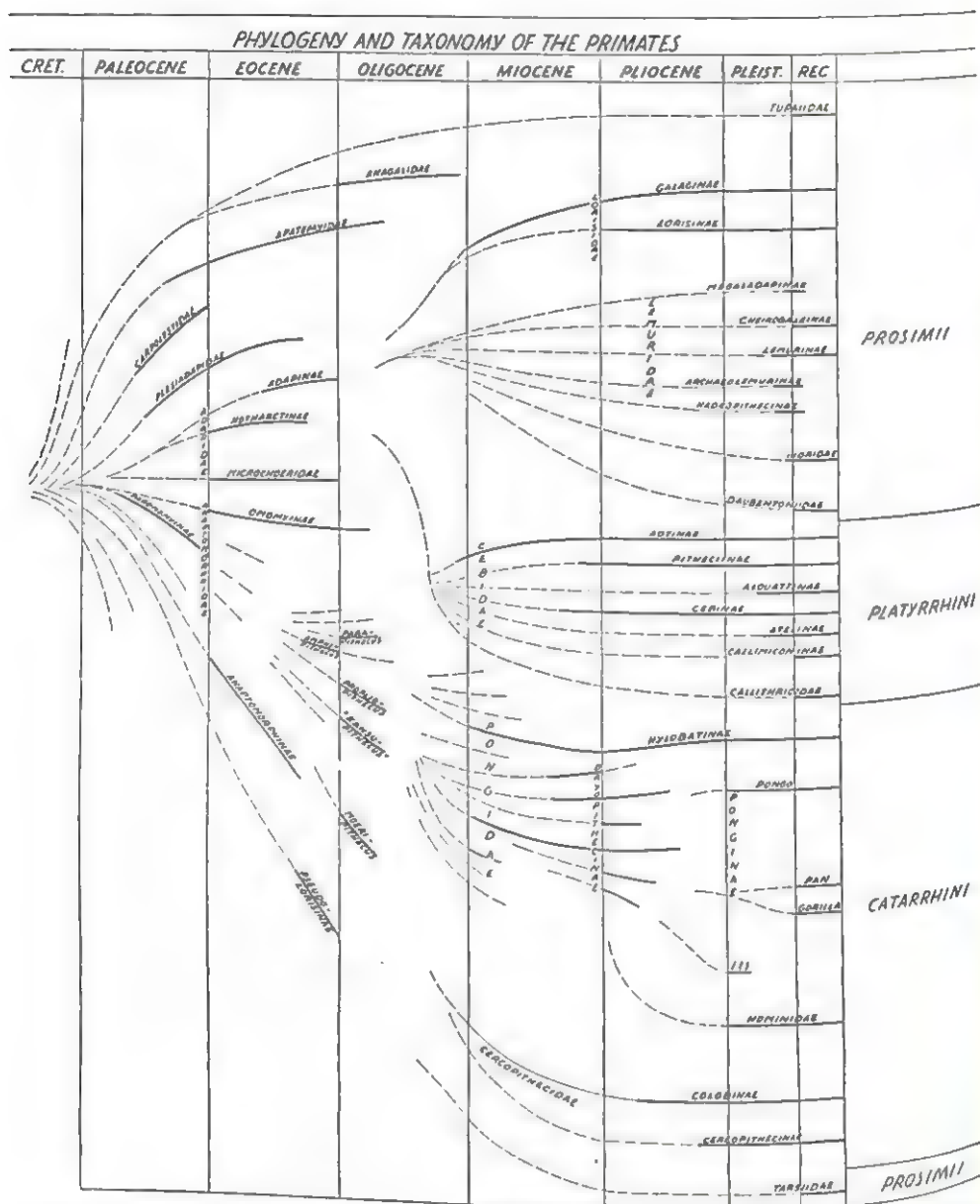


FIG. 3. ANOTHER VIEW OF PRIMATE PHYLOGENY. KNOWN RANGES ARE SHOWN IN SOLID LINES, STARTING WITH THE EARLIEST FORMS THAT CAN BE REFERRED WITH ASSURANCE TO A PARTICULAR GROUP.

we know next to nothing about this earliest therian radiation, but we can infer that it took place—the diversified mammals of the Early Paleocene certainly did not come into existence overnight. “Proto-primates” and “para-primates” surely formed part of it. Tupaioids, macroscelidids, perhaps apatemyids may have appeared at about this time, together with such poorly known groups as the adapisoricids and metacodontids.<sup>4</sup>

Out of this radiation, possibly even a part of it, came the prosimian complex of the Paleocene and Eocene. If the dentition is any guide, these forms were a highly diversified lot, and it is possible, as Barth has suggested, that they were not all arboreal but may have filled a number of ecologic niches open to small mammals, particularly in Paleocene and earlier Eocene time. This prosimian radiation seems to have largely ended with the Eocene, at least in regions from which we have reasonably good fossil records. The rise of modern types of rodents and of carnivores, which occurred about this time, may have been a contributing factor, but more important, probably, was the rise of the catarrhines. Tupaiids, lorisids, and tarsiids have managed to survive the catarrhine inundation, but only by adaptation to ecologic niches in which they have escaped from competition. The only later Cenozoic prosimian expansion, that of the lemuroids, is the result of an accident. African prosimians, perhaps adapines, reached Madagascar (a region to which no non-hominid catarrhine, and indeed few mammals of any sort, ever penetrated), possibly in Oligocene time and certainly by overseas transport, and there gave rise to the profusion of Recent and Late Pleistocene forms for which the island is so justly famous.

A point to be made here is that the Paleocene and Eocene forms, not the terminal twigs that survive today, were the “real” Prosimii. As noted, the early forms have much in common structurally, and constitute a reasonably compact group. As regards taxonomy, I would heartily agree with Simpson that it is preferable to include all, both early and late, in one suborder.

If I may be pardoned a digression into the New World, the platyrrhine radiation, like the lemuroid, was also the result of an accident of dispersal, this time from North America. The South American fossil record permits the assumption that the date was in the first half of the Oligocene. As Gregory has suggested, the ancestral forms may possibly

<sup>4</sup> The last, a North American group, may be represented in the European Eocene by “*Adapisorex*” *anglicus* Forster Cooper.

have been notharcetines, but this is very uncertain. A peculiar fact concerning the platyrrhines is that we have no good evidence that they ever evolved predominantly ground living types, despite the fact that the general situation, absence of placental carnivores, etc., would seem to have been more favorable in South America than in the Old World. This appears to be one more instance showing that the existence of an evolutionary opportunity does not insure that it will be seized. In figure 3, the lines of descent of the various ceboid sub-groups are projected very nearly to the presumed date of ingress. Theory and an excellent example from another order may be cited in support. As Wright ('49, p. 387) has remarked: "When . . . unoccupied territory is reached, a very extensive and rapid adaptive radiation should follow under the divergent selection pressures toward exploitation of the various special ecological niches, opened up by . . . the mere absence of competition . . ." The caviomorph rodents, whose ancestors reached South America by accidental means at about the same time as those of the platyrrhines, illustrate this perfectly, their major subdivisions becoming established almost from the start.

The fact that South American primates had an ancestry distinct from that of the catarrhines since at least the Early Eocene, taken together with their morphological peculiarities, entitles them, I believe, to subordinal rank. Retention of the time-honored terms *Platyrrhini* and *Catarrhini* would appear to be justified.

The catarrhine radiation, the most important from our point of view, began before the end of the Eocene. Beyond this important fact we know almost nothing, due to the fragmentary nature of the few known Late Eocene and Early Oligocene specimens and the lack of any records from the Middle and Late Oligocene. The cercopithecoid-hominoid dichotomy occurred before the Miocene but just when we do not know. Very successful in their own sphere, cercopithecoids clearly had nothing to do with the ancestry of any other catarrhine group, and need no further consideration here.

In reading the descriptions and discussions of the Miocene hominids, it is possible to detect here and there a note of surprise concerning the evidence that they seem to have possessed a quadrupedal gait. The catarrhine radiation was a fairly late one, geologically speaking; the ancestral forms were certainly quadrupedal, and it is therefore not too remarkable that the earlier hominoids should also have been to an extent quadrupedal or that some, at least, remained so into Pliocene time.

The new discoveries in fact deal a death blow to some old arguments concerning the origin of man, arguments which appear to have stemmed from typological thinking. Gibbons have rather distinctive molars, and because of this it is possible to trace a phyletic thread back from the present that does not get lost in the dryopithecine tangle. The Early Oligocene *Propliopithecus* could on this evidence be an ancestral gibbon, and has often been so regarded. As a result, a train of reasoning something like this appears to have prevailed in some quarters: living gibbons are brachiators par excellence; *Propliopithecus* was a gibbon, ergo it was an excellent brachiator; the ancestral pongines must have been too; man does not brachiate, ergo his ancestors must have branched off before this adaptation became established; *Propliopithecus* is Early Oligocene in age, ergo the Hominidae arose in the Eocene; Q. E. D. The new evidence, which rather strongly suggests that extreme specializations in locomotion occurred quite late in hominoid history, does away with this old objection to close affinity between hominids and pongids. Proponents of this affinity no longer have to combat the contention that a radical change in the direction of adaptation would be necessary in order to derive the one from the other. The concept responsible, basically, for the old arguments against such derivation was the notion, once rather prevalent, that all parts of animals evolved at about the same rates, a view repeatedly shown to be erroneous.

The generalized locomotor apparatus of later Tertiary hominoids has been hailed as showing that man's ancestry did not pass through a brachiating stage, hailed almost with relief, as though brachiating were some deadly sin. I submit that this is going too far and that there is no real evidence for it. The objections to such a stage perhaps stem in part from old views and may also be in part semantic—the word brachiation being associated with the extreme conditions in living pongids. There would seem to be nothing in the known structure of the earlier pongids to indicate that they did not brachiate to some extent, and, as Gregory has long insisted, a moderate amount of brachiation seems to be the best explanation of how the hominid line got up on its hind legs. Our ancestors, however, unlike those of the living pongids, were able to take their brachiation or leave it alone. The extreme degree of this adaptation shown by hylobatines and pongines today may be as recent an event in primate history as acquisition of the upright gait.

Some recent authors who favor an origin of the human stock from



the pongid, branch us off in the Early Miocene, if not earlier, again perhaps in an effort to avoid the demon brachiation. In figure 3, this event is postulated to have occurred considerably later. In view of the rapid evolutionary progress made by the hominid line during the Pleistocene, there seems to be no compelling reason for assuming that the earlier stages should have required longer than the 10 million years or so allotted to the Pliocene. Man is the result of an adaptive shift in the direction of evolution, and such events are rapid, geologically speaking. But man is a non-non-hominid primate and I must not discuss him further.

These are the ideas of one paleontologist concerning the reasonable suggestions that paleontology can make about primate history (novelty for any of them is, of course, disclaimed). They are as tentative as our story is incomplete, but the history of primate discovery holds forth the promise of a far better base on which to build. Vertebrate paleontology is roughly 150 years old. By the end of the first third of this period, say up to 1859, only 7 extinct genera of primates had been described. Between 1860 and 1900, 21 more were added (these figures are for the world); between 1901 and 1925, 33 and since 1926, 46. If this can be kept up, we should be well off some day, but in the meantime we are not getting the most out of what we have. Professor Straus recently remarked that it would be nice if good casts of the australopithecines were generally available. I should like to go further and say that casts or photographs of all important fossil primate specimens should be prepared and made widely available for exchange or purchase. With existing media, especially latex, magnificent casts can be made. Stereoscopic photomicrographs from various aspects would serve for small and delicate specimens. This sounds like an ambitious program, but it seems a good way to avoid more *Oreopithecus* incidents. If, then, we can continue the rate of discovery and provide for wide use of the materials we have and hope to get, our grandchildren will perhaps have the beginnings of a workable outline of primate phylogeny, and on this properly qualified note of optimism this brief presentation may be closed.

# LITERATURE CITED

- ABEL, O. 1927 Lebensbilder aus der Tierwelt der Vorzeit. Gustav Fischer, Jena.
- BARTH, F. 1950 On the relationships of early primates. Am. J. Phys. Anthrop., n. s. 8: 139-149.
- BOHLIN, B. 1946 The fossil mammals from the Tertiary of Tabun-buluk. Rept. Sino-Swed. Scient. Exped. N. W. Prov. China. 6: no. 4.
- 1951 Some mammalian remains from Shih-ehr-ma-ch'eng, Hui-hui-p'u area, western Kansu. Ibid. no. 5.
- HOOLJER, D. A. 1951 Questions relating to a new large anthropoid ape from the Mio-Pliocene of the Siwaliks. Am. J. Phys. Anthrop., n. s. 9: 79-94.
- HÜRZELER, J. 1948 Zur Stammesgeschichte der Necrolimuriden. Schweiz. Pal. Abhandl. 66(3): 1-46.
- 1949 Neubeschreibung von *Orcopithecus bambolii* Gervais. Ibid. 66(5): 1-20.
- 1949 Über die europäischen Apatemyiden. Verh. Schweiz. Naturf. Ges. 129: 140-141.
- SCHULTZ, A. H. 1953 Man's place among the primates. Man, 53: 7.
- SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. Ibid., 85: 1-350.
- 1947 Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Am. 58: 613-687.
- 1949 The Meaning of Evolution. Yale Univ. Press, New Haven.
- TEILHARD DE CHARDIN, P. 1916-1922 Les mammifères de l'éocène inférieur et leurs gisements. Ann. Paleont. Paris. 10: 171-176; 11: 1-116.
- WEITZEL, K. 1949 Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozän von Mersel bei Darmstadt. Abh. Senckenb. naturf. Ges. no. 489, 1-24.
- WRIGHT, S. 1949 Adaptation and selection. In Genetics, Paleontology and Evolution. Princeton Univ. Press, Princeton, N. J., pp. 365-389.
- ZAPPE, H. 1952 Die Pliopithecus-Funde aus der Spaltenfüllung von Neudorf an der March. CSR, Verh. Geol. Bundesanst., Wien. Sonderheft C: 126-130.





COMPARATIVE ANATOMY OF NEW WORLD  
PRIMATES AND ITS BEARING ON THE  
PHYLOGENY OF ANTHROPOID  
APES AND MEN  
(ABSTRACT)

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THE platyrrhine primates, long slighted as a side issue in the study of human evolution, have a peculiar relevance to that study by virtue of this very isolation. Independently evolved from Eocene lemuroids or tarsioids, the New World monkeys have developed a remarkable series of features closely paralleling those developed in the Old World radiation. The aspects of this parallelism most significant for the study of the evolution of anthropoid apes and men are those related to their locomotion and posture. In addition to the platyrrhine counterpart of the catarrhine monkey, the New World radiation produced three genera (*Ateles*, *Brachyteles*, and *Lagothrix*) capable of brachiation and displaying certain adaptations to upright posture.

A comparison of the structural correlates of brachiation in Old World and New World primates provides a revealing technique in attempting to distinguish genetic from adaptive resemblance in closely related living forms and aids in the reconstruction of form and function in fossil relatives. In the present study a more precise definition of brachiation has been sought and contrasts have been made with typical arboreal quadrupedal locomotion and terrestrial bipedalism. This involves an analysis of the proportionate lengths of limbs and their segments and a comparison with trunk lengths, the proportions and articulations of the thoracic and lumbar spine regions, and the adaptive mechanisms in the musculo-skeletal structure of shoulder and hand.

A full appreciation of the significance of this parallelism must await further study of these little known primates.



## PRIMATE EVOLUTION FROM THE VIEWPOINT OF COMPARATIVE ANATOMY

BY D. DWIGHT DAVIS

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PHYSICAL anthropology, in so far as it deals with comparisons of the structure of the primates, is a branch of comparative anatomy. The goals, the limitations, and the methodology are then those of comparative anatomy. It may therefore be profitable to consider physical anthropology against the broader background of comparative anatomy, to see whether it has kept pace with development in the parent field.

I am not an anthropologist, and I therefore have no anthropological tradition to prejudice my views. The fact that I am not an anthropologist also implies, of course, that I am grossly ignorant of the details of this science. In this review we are not interested in details, however, but in general principles—which may easily become blurred or even obscured if we are too much preoccupied with details.

Let us begin by considering very briefly the history of comparative anatomy, since changing fashions in comparative anatomy would be reflected in interpretations of primate evolution.

### THE EVOLUTION OF COMPARATIVE ANATOMY

Comparative anatomy is one of the oldest scientific disciplines, and its aims and concepts have undergone considerable changes. These were not random changes in direction. On the contrary, they follow a definite pattern. In part they reflect the evolution of general scientific concepts, and in part the growth of morphological knowledge itself. No real understanding of comparative anatomy is possible unless these shifts in purpose are appreciated.

Until the middle of the nineteenth century the goal of comparative

anatomy was to discover the several "ideal plans" that were believed to underlie the structure of organisms. It is difficult to appreciate the viewpoint of this by-gone era, when the concepts of historical change and blood relationship between species had not yet entered biological thinking. The ideal plans were formal abstractions, devoid of meaning to their discoverers, except to those devout Christians to whom they represented the master blueprints of the Creator. Linnaeus, when he placed man in his order Primates, certainly was not thinking in terms of blood relationship. Like the structure of crystals, or the periodic table of the elements (as then understood), the common plans represented only ordered systems. This concept is best seen in the works of Cuvier and others of the eighteenth and early nineteenth centuries. This period in the evolution of comparative anatomy produced an immense body of factual data that was incorporated into the period that followed. Its most important achievement was the concept of homology and analogy, developed by Owen, which is still the basic tool of comparative anatomy.

Looking back from the vantage point of today, it is incredible that the simple and obvious interpretation was not seen—that common structure is a product of common ancestry. Yet the history of science shows that such mental blocks are not uncommon; we need recall only the equally remarkable history of the phlogiston theory, which held thinking in chemistry and physics enthralled for centuries.

The dramatic shift in the goal of comparative anatomy immediately following the publication of the *Origin of Species* in 1859 is too well known to need more than passing mention. Almost overnight, once the idea of descent with modification was grasped, comparative anatomy was completely re-oriented. The goal then became to discover the history of the structural elements of the animal body, and thus of the organisms themselves; in other words, the portrayal of the true course of phylogeny. *This is the theme of every textbook of comparative anatomy in use today, and the motivation of nearly all research in this field.*

This is a sterile aim. Classical comparative anatomy has never gone beyond inferring and describing the temporal sequence of biological events, and this is merely systematized knowledge. Dr. James B. Conant recently contended that systematized knowledge does not of itself constitute a science, that such knowledge is significant only as it gives rise to new ideas or concepts. This seems to me to be a valid criterion, and it is precisely at this point that classical comparative anatomy failed. If the concepts of Gegenbaur, Wiedersheim, and their spiritual descen-



dants are the final chapter in the evolution of comparative anatomy, then this science deserves all the hard things that have been said about it. The central problem of historical biology is to explain, not to describe, the historical events that produced the bewildering diversity of living organisms that inhabit the earth today.

Essentially all modern biologists have abandoned belief in any of the mystical drives that have been suggested as forces in evolution. The evidence is overwhelming that evolution is non-purposive and non-directed, that it is opportunistic, based on probabilities. At every stage in a given lineage alternative courses were open and the one actually followed was determined in each instance by the interplay of random genetic factors in the breeding population on the one hand, and the complex of factors in the environment on the other. The factors that determined shifts in adaptive direction may have been, and probably usually were, very trivial at the outset, however far-reaching their ultimate results. Each lineage is thus the result of a continuous but constantly changing complex of probabilities, an organism-environment relationship so precariously balanced as to suggest that evolution is truly indeterminate, that if the whole show could be run off again the outcome would not be the same, and might indeed be very different.

On such an indeterminate view, phylogeny is merely a pattern of what *did* happen in one particular case, merely one of an enormous number of possible patterns that could have resulted under identical circumstances. Phylogeny looks orderly and purposive, like the unfolding that the word "evolution" implies, but actually it looks purposive only in retrospect. Past events determine future events in evolution, not directly and absolutely, but only by altering future probabilities. The difficult problem of discovering how this enormous complex of shifting probabilities works can be solved only by analyzing how it did work in a great many cases. William Wightman, in his recent book *The Growth of Scientific Ideas*, called form, the subject matter of comparative anatomy, "a plastic record of the history of organisms." The broad goal of comparative anatomy should be, I believe, to attempt to interpret the why of this plastic record by considering it against the factors that are known to determine form. This includes pertinent data from genetics, experimental embryology, paleontology, ecology—a synthesis, in short, of all biological data that bear on the question of form. In less ambitious projects—the phylogeny of man or of a species of bear, for example—the principle is still the same; it is more important to know

why a particular direction of evolution was followed than merely to know the direction.

This involves a considerable re-orientation of the aims and methods of comparative anatomy.

#### THE NEW COMPARATIVE ANATOMY

Two ideas have deeply affected the recent thinking of comparative anatomists. Neither was a product of morphological research. The first was the suggestion, made originally by Goldschmidt ('27), that the timing and rates of developmental processes are gene-controlled. This provided a mechanism whereby individual genes, by controlling patterns of differentiation and growth, may affect whole morphological units, in addition to the genes that control the individual "characters" with which the experimentalist is usually concerned. This kind of gene effect is difficult to demonstrate experimentally, because changes in early morphogenetic processes usually have lethal consequences. It has been established by a considerable body of evidence, however, both experimental and observational. I reviewed the subject briefly elsewhere (Davis, '49). I believe that the importance of this concept to comparative anatomy cannot be exaggerated.

Each of the major taxonomic categories represents an adaptation to a particular way of life, to exploiting a particular ecological opportunity. The phyletic evolution of such an adaptive type is relatively easy to understand; it is the *origin* of major adaptations that presents difficulties. In most cases the major adaptation is quite obvious: the bats for flight, the carnivores for predation, the whales for swimming. Even at lower taxonomic levels the adaptive relations are often clear-cut: the vampire bats for blood-lapping, the nectar-feeding bats for extracting nectar from flowers; the dogs for running down their prey in packs, the cats for pursuing theirs alone and by stealth. It is remarkable—and unfortunate from our standpoint—that the primates, almost alone among the large and successful orders of mammals, are not characterized by an obvious and clear-cut major adaptation.

The second idea was the morphogenetic field concept, which is a corollary of the first. The morphogenetic field concept makes it possible, in many cases at least, to reconstruct the history of the genetic changes that underlie major adaptations. If such major morphological units as the whole molar toothrow, the whole thoracolumbar section of the verte-

bral column, or the whole masticatory musculature, are each subject to some sort of unitary control in addition to the detailed gene-character relations familiar to experimentalists, then the building blocks of evolution may be enormously simplified. Techniques can be developed for detecting morphogenetic fields where they cannot be delimited experimentally, and phylogenetic changes in terms of these units can be traced. If shifts in adaptive direction frequently involved such units as this, I believe we are, as morphologists, little concerned with the minor polishing of the basic adaptations, or with the mere multiplication of "characters" that is usually involved in speciation. The important, decisive events are the ones that set the stage for exploiting new ecological opportunities. Apparently they often have "trigger" or "threshold" effects that under favorable conditions may result in a period of explosive evolution. They also, of course, restrict and delimit the future possibilities of the lineage. An important aspect of such phenomena is that they can be seen to be preadaptive only in the light of subsequent events. At the outset of a new adaptive relationship the possible workable organism-environment relationships are so numerous and depend so heavily on chance, and the factors initially tipping the balance in a given direction are often so trivial, that prediction is impossible.

Statisticians point out that generalized effects would be far less likely to become established in a breeding population than would accumulations of many small deviations screened by natural selection. Relatively major phenotypic effects have therefore been practically dismissed from consideration as a factor in evolution. There is considerable evidence, which seems to me incontrovertible, that such effects did play a part, and I don't see how it can be ignored.

This dynamic approach to comparative anatomy has scarcely been tried. It is much more difficult and tedious than the familiar study of phylogeny. It involves techniques and disciplines that are unfamiliar to anatomists. The results, however, are vastly more rewarding.

#### THE METHOD

It has long been customary to recognize two distinct elements in the morphology of an organism: the "heritage" characters inherited from its ancestors, and the "habitus" characters that are correlated with its particular way of life. This simple dichotomy can be expanded into a hierarchy in which the habitus characters of yesterday become the heritage characters of today. For example, some of the heritage charac-

ters of the Hominidae obviously were the habitus characters of the common ancestor of the superfamily Hominoidea, in which they represented the new major adaptation of the man-anthropoid ape stock. Some of the heritage characters of the Hominoidea, in turn, were the habitus characters of the common ancestor of the suborder Anthropoidea, and so on back to the habitus characters (the basic vertebrate adaptation) of the subphylum Vertebrata, and even beyond.

This sorting of the new from the old is basic to any understanding of the morphology of an organism. It is, of course, the basis for our system of classification. It warns us, for example, that the closed orbits, the molar structure, the opposable thumb, and many other features of man are not strictly human characteristics. This warning is often unheeded in practice, and attempts are made to interpret the anatomy of an organism as if an engineer had designed it from scratch, specifying materials and sub-assemblies purely on the basis of functional requirements.

I regard this sorting as the first step in deciphering the mechanism whereby a given terminal condition was achieved in evolution. It separates out those conditions that represent earlier adaptations inherited from a long line of ancestors. This step might be formulated as:

(1) *In what respect does the morphology of the species or group under consideration differ from the next more generalized condition?*

This step involves straight comparison of form, the familiar procedure of classical comparative anatomy. It is at this point that classical comparative anatomy stops. But this is only a first step, because it is only those features that are directly subjected to selection pressures that are significant in adaptation. Among the numerous differences we have segregated in our first sorting there are almost certainly some not directly related to the new functional requirements. These may be merely indifferent. In snakes, for example, the anal plate may be either single or divided in closely related genera, and it is difficult to conceive of any functional significance in this. The exact tail length of many short-tailed mammals very probably has no relation to habits. There are also secondary adjustments resulting from functionally important changes in adjoining parts. For example, I have studied mammals in which the orbit is depressed far below its normal position, producing remarkable alterations in the Frankfort plane. These were forms in which the temporal muscle was enormously enlarged, however, and it was the expansion

of this muscle that crowded the orbit downward, not an adaptation involving the eye. Finally, there may be differences without functional significance that result from a genetic tie-up with another structure that is functionally important.

It is, of course, impossible to prove that a given condition is not related in some obscure way to the functional requirements of the animal. Careful attention to architecture and engineering, and above all detailed knowledge of the habits and behavior of the animal will, however, often reduce the probability almost to zero.

The second step may be formulated:

(2) *Which of the observed differences are directly related to the different functional requirements of the derived form?*

The functionally important features we have now isolated still are not limited to those under direct genetic control. Many morphological features, although functionally of the greatest importance, are only developmental consequences of other features that are under direct genetic control. In the absence of the primary structure such secondary features fail to appear. They may be described as "genetically determined once removed," since in the end their appearance or non-appearance does depend on genetic factors. The surface modelling on bones, for example, is determined by muscles and tendons rather than by genes acting directly on the bones, and most of the detailed architecture of bones is a non-genetic response to stresses and strains. When endocrine actions are involved, as in the enlarged sagittal crest of the male gorilla, the genetic basis for hypertrophy of the crests may be twice removed. In all cases, of course, the range of response is not unlimited, and is presumably genetically controlled. That a particular feature of a structure is not under direct genetic control can be determined by observation, but only experimentation can prove that a feature is genetically controlled. Without experimentation genetic control can only be inferred.

The third step may be formulated:

(3) *Of the differences directly related to new functional requirements, which are under direct genetic control and which are merely developmental consequences secondarily related to the genetic substrate?*

The fact that a functional element is under direct genetic control does not of itself guarantee that selection acting on the element is responsible for the observed condition of the element. Development of



a structure may, for example, be achieved via a differential growth rate. The growth pattern may have produced a close adaptive relationship at the time it was introduced. But if subsequent selection is for increased organism size, then the special structure will, because of its exponential growth rate, increase in size and/or complexity at a faster (or slower) rate than the entire organism. With increasing size, selection will usually be increasingly negative for the special structure, until an equilibrium between this negative selection and positive selection for total organism size is reached, or until the organism reaches the optimum size limits set by other factors.

Exponential growth rates by their very nature tend to produce developments so spectacular that they seem to demand functional explanations. Yet we know that the enormous antlers of moose and of the extinct Irish elk have gone beyond the stage of maximal usefulness. I find that the development of the dentition of the huge cave bear fits into an exponential curve based on skull size. I suspect that the grotesque nose of the male proboscis monkey (*Nasalis*) has a similar basis rather than representing a product of sexual selection. Developments such as these may have no positive relation to the requirements of the animal, however conspicuous and characteristic their form may be. Their genetic roots may lie far back in the ancestry of the organism we are studying.

Having localized in the morphology of our sample those features that represent the primary results of natural selection, the adaptive features resulting from the interplay of a particular environment and a particular genetic substrate, what can we do with them? I find that in the Carnivora the number of such features remaining after the final sorting may be surprisingly small, perhaps as few as half a dozen. We probably never will know the exact genetic mechanism behind such adaptive specializations, although in favorable cases even this can be inferred. At the very least we have localized the important elements of the evolutionary mechanism that were involved in a specific case. At best we have shifted our viewpoint from a comparison of static structure to the dynamic processes that determine structure.

Finally, the morphology of an organism cannot be interpreted except in the light of all of its antecedents. Any phyletic line represents a succession of adaptive relations. Earlier adaptations, particularly the morphogenetic processes whereby they were achieved, may have the most profound and unexpected repercussions many generations and many

adaptive relations later. If as a non-anthropologist I may venture a suggestion as to what seems to me the most desirable step in attempting to understand the evolution of man, I would recommend studying the treeshrews—and even the generalized insectivores. To me it is incredible that these creatures, in which the decisive steps leading to man may already have been taken, are almost unknown while we continue to lavish our attention on the higher primates.

Knowledge of structure without corresponding knowledge of function is sterile, and I should like to see a project, similar in scope to Carpenter's ('34; '40) work on the gibbons and howling monkeys, set up to study the habits and behavior of the Tupaiidae.

#### LITERATURE CITED

- CARPENTER, C. R. 1934 A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comp. Psychol. Monog.*, 10: 1-168.
- 1940 A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Monog.*, 16: no. 5, 1-212, 30 pl.
- DAVIS, D. D. 1949 Comparative anatomy and the evolution of vertebrates. *In*: Genetics, Paleontology, and Evolution, Ed. by G. L. Jepsen, G. G. Simpson, and E. Mayr. Princeton Univ. Press, Princeton, New Jersey.
- GOLDSCHMIDT, RICHARD 1927 Physiologische Theorie der Vererbung. Springer, Berlin.





## A COMPARATIVE FUNCTIONAL ANALYSIS OF PRIMATE SKULLS BY THE SPLIT-LINE TECHNIQUE \*

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THE mammalian skull serves to house and protect the brain and the organs for the special senses of sight, hearing, taste and smell; to provide inlets for food, water and air, plus passageways for blood vessels and nerves; to provide for biting and chewing food, and at the same time to give attachments for the chewing muscles and a bony framework to resist the forces that are set up by the masticatory apparatus; and to give attachment for the muscles which move the head and maintain its carriage. In order to survive the animal must be able to have all these functions operating in harmony. It is probable that compromises between them are in places necessary. It is certain that they can affect each other in some degree.

The skull must therefore be thought of in terms of its relationship to many bodily functions, realizing that it is affected by many factors. This complexity is partly counterbalanced by its remarkable geographic character, by which the location, interrelationships and operations of many vital organs can be deduced. As examples, the roof of the mouth is the floor of the nose, and the origins and insertions of chewing and head-moving muscles frequently leave their marks on the bone, allowing an evaluation of their strength and the direction of their contraction. The value of the skull for analysis of vital processes is most vividly illustrated in the paleontological record, where it is possible to make

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meaningful comparisons between the skulls of animals which we have never seen alive. However, progress in the interpretation of the evolution of the skull must depend in large part on the methods of analysis available on living forms, and the development of new techniques is vital to the advancement of biological science as a whole.

The bone in the skull has other levels of organization not observable in the gross structures, offering methods of analysis which carry beyond those of ordinary observation. One promising aid to functional analysis is the split-line technique. It demonstrates the organization of the compact surface bone by staining methods. Benninghoff ('25) was able to show in a human skull that some areas of the bone, such as in parts of the face, were organized in their split-line patterns while other areas, such as the skull-cap, were not.

The technique is described extensively elsewhere (Seipel, '48; Tappen, '53). The bone is decalcified in dilute acid until it is soft and rubbery enough to allow easy penetration by a needle. Usually splits result rather than round holes, because bone has a minute "grain" analogous to that of wood. India ink is then put into the fissures to clarify their direction. Benninghoff ('25) and Seipel ('48) showed histologically that the splits correspond to the direction of organization of the majority of the Haversian systems in the region punctured. Haversian systems are the basic means of supplying blood to compact bone. They consist of very minute central blood vessels with concentric layers of bone called "lamellae" surrounding them.

Benninghoff and other workers used intermittent punctures in producing their split-lines. This gave an incomplete picture, since branchings, divergencies and the meeting points of different split-line systems could not be accurately traced. There is reason to believe that they were at times led into errors of interpretation because of the inadequacy of their technique. Seipel ('48) made a great improvement by joining his split-lines with further intermediate punctures in those regions in which patterns were distinct enough to warrant it. This method was followed in the present study.

In well-organized regions it was found that a further refinement was possible. The point of the needle was pushed into the bone two millimeters or less, then pulled in the direction of the original split. In this way long split-lines could be made quickly, and the actual deviations of the Haversian system organization could be traced more accurately. It was also found that directional organization in regions

of very thin bone could be ascertained in this manner, where punctures with needles of even very thin diameter frequently gave no pattern, presumably because of the crushing effect. It was thus possible to obtain patterns in such regions as the tooth sockets in small specimens.

It is necessary to use this innovation with caution. Frequent tests were necessary to make certain that the needle would go only in one direction. In only one region of one specimen was it found possible to pull the needle in almost any direction.

In an earlier work (Tappen, '53) it was found that decalcification affected the teeth more than other parts of the skull, destroying the enamel very quickly. In order to preserve the appearance and continue study on the occlusal relationships of the specimens, dental beewax was melted and used to cover the teeth, sealing them off from the acid. This method is also recommended to workers interested in keeping parts of skulls intact while decalcifying other parts.

The biological meaning of the Haversian system organization revealed by the split-lines is far from being completely understood. Theoretical discussions may be found in Benninghoff ('27), Murray ('36) and Seipel ('48). Work along these lines has been sporadic, mainly descriptive, and has been accompanied by little experimental work to determine causes. The general assumption has been that they are somehow related to mechanical forces, pressure and tension, which are acting upon the bone. As will be seen, this assumption makes a good deal of sense in some areas of primate skulls, but other areas are not readily explained on this basis and other factors seem to influence the direction of the lines.

Some of the most indicative investigations are those in which split-line preparations were made on bone which suffered functional alteration during life. Benninghoff ('27) found changed patterns in a femur bent by rickets, and Seipel ('48) found that the patterns in a mandible, broken and imperfectly reset, adapt their direction to the change. It thus appears that split-line patterns can actively change during the life of the individual. Definitive controlled experiments have not been made, however.

In order to proceed from the relatively familiar to the unfamiliar, and to maintain the basic orientation of this non-human primate symposium on problems relating to man, the split-line pattern in the human face may be briefly described. Figure 1 is from Tappen ('53). The pattern of lines immediately above the tooth row parallels the alveolar



margin. Immediately above, all the lines in the face ascend, the ones from the molar region paralleling the zygomatico-alveolar crest and the others tending to parallel the nasal opening. These divergent systems are interrupted by a continuous system of lines beginning at the frontal process of the maxilla, coursing along the infraorbital region and continuing through the zygoma to the region of origin of the anterior tendinous portion of the masseter muscle. This has been interpreted as meaning that the pull from the muscle is of primary importance in counteracting the stresses from the pressure of the tooth row, and that the infraorbital, zygomatic and lateral orbital regions are primarily

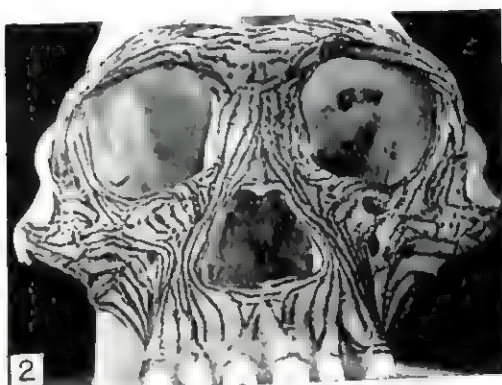


FIG. 1. SPLIT-LINE PREPARATION ON HUMAN FACIAL SKELETON.

FIG. 2. SPLIT-LINE PREPARATION ON CHIMPANZEE FACIAL SKELETON.

under tension from the downward pull of the exterior chewing muscles. This is in direct opposition to the generally expressed view (Hooton, '46) that the lateral orbital and brow ridge area resist upward chewing pressures. It may also be noted that the human brow ridge shows little or no organization. From this kind of information it was postulated that structures such as the infraorbital bar represent functional responses to stress while such structures as the brow ridges probably do not.

The chimpanzee patterns, shown in figure 2, differed strongly enough from those in man to suggest correlations with differences in gross structure and with relationships between different parts. Specifically, there are no completely divergent systems of split-lines in the lower face. Instead of an infraorbital-zygomatic system of lines cutting off the ascending patterns, the ascending lines continually branch off laterally

toward the region of origin of the masseter muscle, the deviation being at a progressively higher level the farther the lines are away from the muscle. Finally, some lines enter the orbit, and others continue up the interorbital region to the brow ridge. These differences may be related to the longer face, absence of elevated nasal bridge, and lower origin of the masseter muscle in relation to the orbits. It is also possible that this clarifies the occasional appearance of the canine fossa in man and its absence in the chimpanzee, since there is implied a relatively unstressed area between three divergent split-line systems in man but not in the chimpanzee. It will also be noted that the split-lines in the chimpanzee brow ridge are strongly marked and continuous with the lines in the lateral orbital region. This has been taken to indicate that the brow area in the chimpanzee is an important stress-bearing structure, and that it resists tension from the downward pull of the temporal and masseter muscles. It is also indicated that this is so because there is no forehead region above the orbits to absorb and distribute these stresses, as is the case in man. In actuality, the chimpanzee face and braincase grow apart during development of the animal. Seipel ('48) has shown that the split-line pattern is already developing in the brow region of a three-year-old chimpanzee, however.

So much data of relevance to the understanding of the primate face resulted from comparative split-line analysis of one ape that work with other non-human primates seemed imperative. Only the chimpanzee has been described in more than the barest features. Accordingly, split-line preparations were made on widely differing representatives of the order. I am indebted to the Wistar Institute of Anatomy and Biology for lending single specimens of *Simia satyrus* (probably male), *Hylobates mulleri* (female), *Macacus cynomolgus* (male), *Semnopithecus femoralis* (sex unknown), *Ateles* (male, species unknown) and *Lemur mongos* (sex unknown). All these animals had full permanent dentition in good occlusion. Mr. Harold Green of the Academy of Natural Sciences, Philadelphia, donated the specimen of a young gorilla, sex unknown. Only the first molars are erupted in the permanent dentition. The preparations include the mandible, braincase and skull base as well as the mid-facial region, although these were done on both sides only when the pattern proved to be very interesting.

Detailed description and analysis of this material must await a later publication. Some of the salient features of these specimens can be reported here within the limits imposed by the time allotted and the

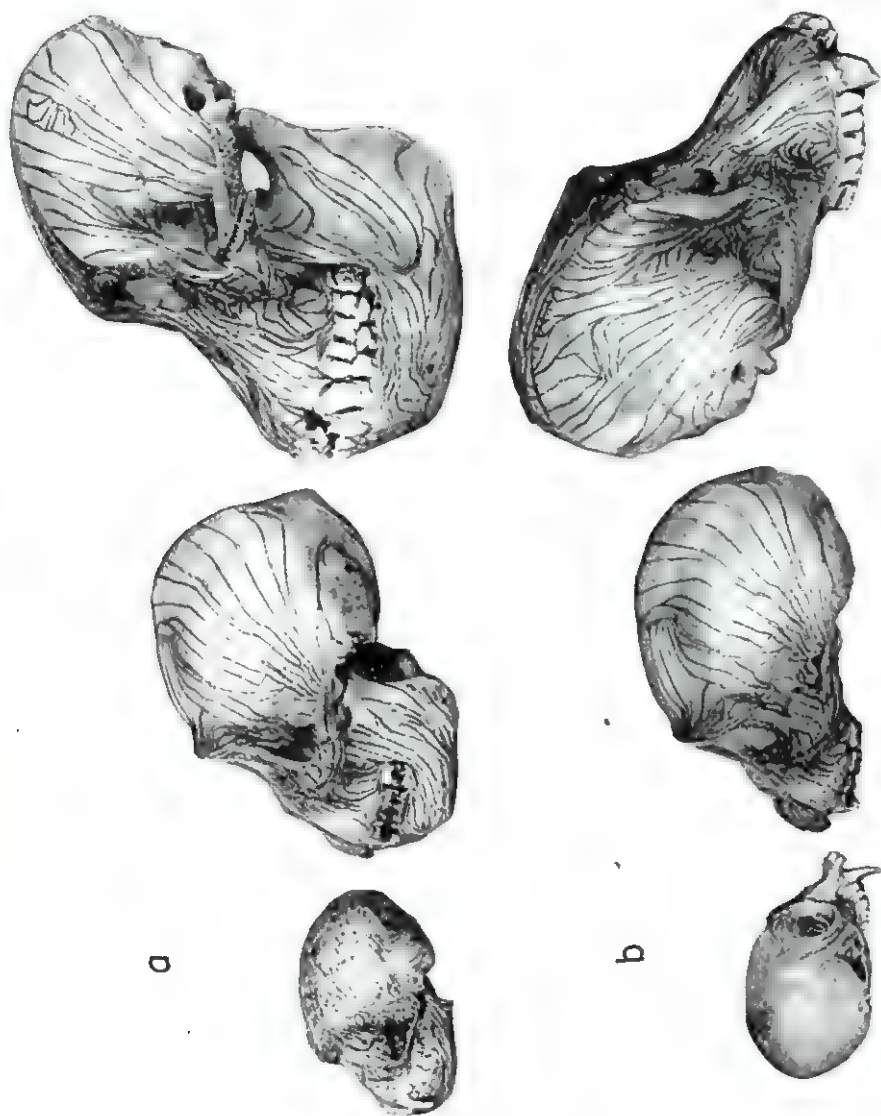


FIG. 3A and B. LATERAL VIEW OF SPLIT LINE PREPARATIONS ON THE SKULLS OF ADULT GIBBON, JUVENILE GORILLA AND ADULT ORANG UTAN.

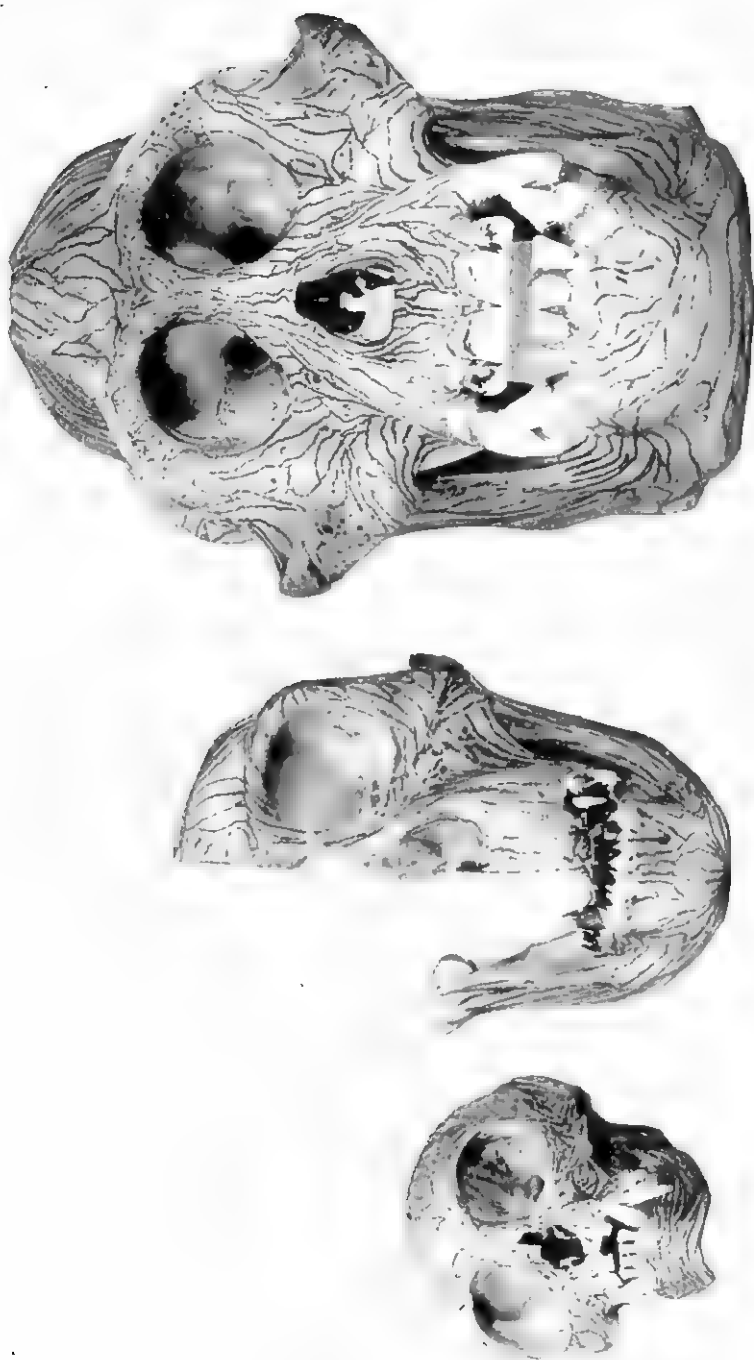


FIG. 4. ANTERIOR VIEW OF SPLIT-LINE PREPARATIONS ON THE SKULLS OF ADULT GIBBON, JUVENILE GORILLA AND ADULT ORANG UTAN.

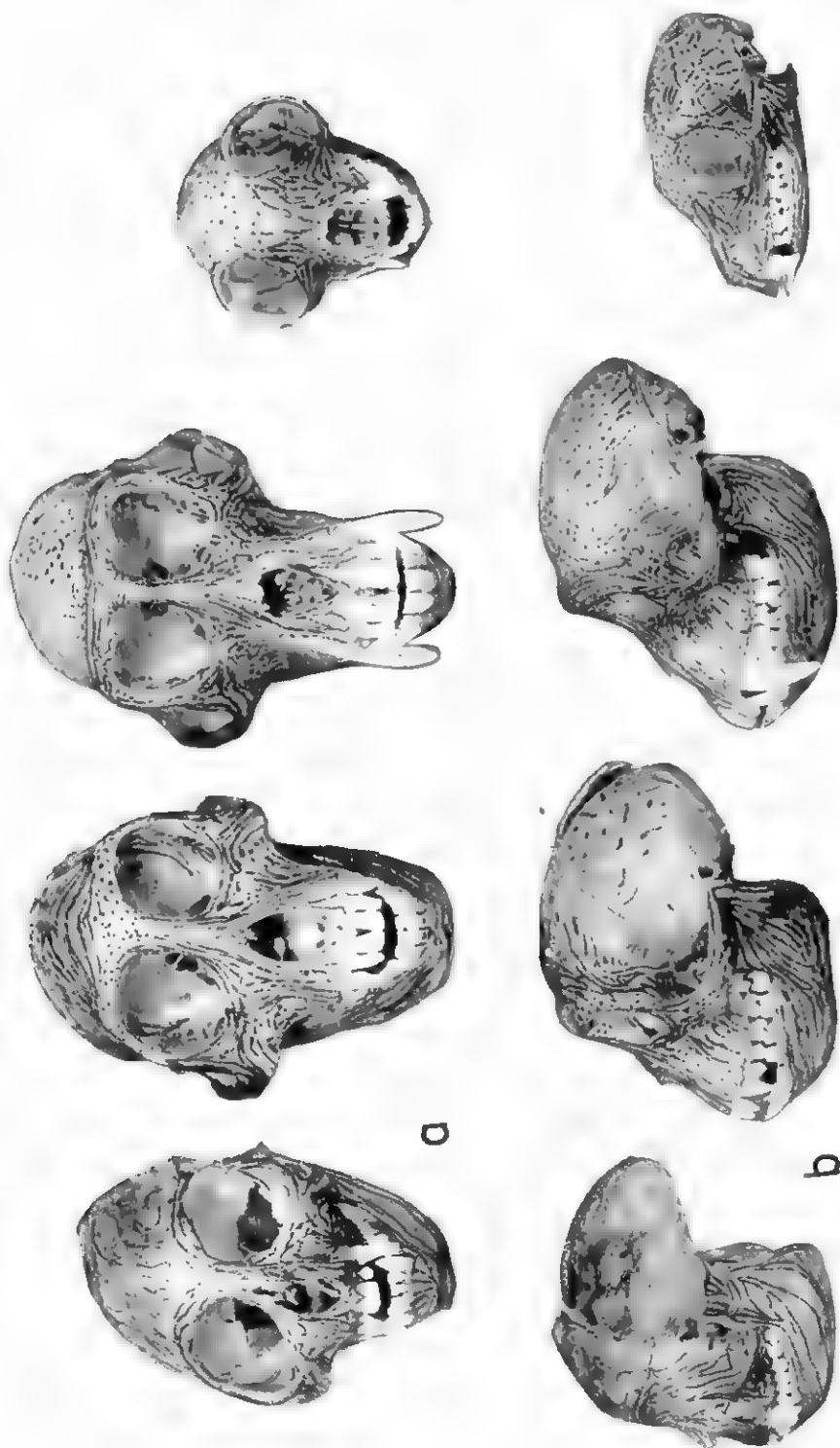


FIG. 5. SPLIT-LINE PREPARATIONS ON THE SKULLS OF SPIDER MONKEY, LANGUR, MACAQUE AND LEMUR.  
A. ANTERIOR VIEW. B. LATERAL VIEW.





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FIG. 6. SPLIT-LINE PREPARATION IN THE BASAL REGIONS OF THE ORANG UTAN CRANIUM.

FIG. 7. SPLIT-LINE PREPARATION ON CRANIUM OF LANGUR, SHOWING ORGANIZED PATTERNS INSIDE THE BORDERS OF THE ORBIT.

FIG. 8. SPLIT-LINE PREPARATION ON MANDIBLE OF SPIDER MONKEY, SHOWING LINES ON BOTH SIDES OF RIGHT RAMUS AND CORPUS. PATTERNS ARE AT RIGHT ANGLES TO EACH OTHER IN THE REGION OF INSERTION OF THE



FIG. 9. SPLIT-LIME PREPARATIONS ON MANDIBLES.

review nature of this article, however. A number of split-line characteristics are relevant to problems raised by the comparisons made between man and the chimpanzee, and other problems are revealed.

Viewed from the side, (figure 3A) the gibbon shows locally organized patterns in the area bounded by the temporal muscle but no overall regularity. This is in a number of respects similar to the human situation reported by Benninghoff ('25), although he found definite patterns associated with the human temporal lines. The orang utan and the gorilla, on the other hand, show continuous lines which appear to correspond generally to the fan-like spread in the direction of the fibers of the temporal muscle. These end at the temporal lines in the orang utan, but merely deviate at this level in the gorilla, continuing to the sagittal suture.

The relationship of this pattern to the pull of the temporal muscle is strikingly evident, but two bilateral deviations from the general picture in the orang utan indicate that factors other than mechanical forces can be acting to organize the bone. (Figure 3B). Well up on the parietal bone a sudden change gives a local area of radiation which may correspond to the direction of growth of the bone from its original ossification center. Ahrens ('36) found that split-line patterns in the human fetal and infantile cranial vault correspond to the direction of growth of the original bone, radiating from the original ossification centers. By the age of seven years, however, the lack of organization in the adult observed by Benninghoff ('25) was already apparent. The other deviation from the general pattern corresponding to the temporal muscle may be observed in the frontal bone as it meets the lower part of the parietal. Here the split-lines turn toward the suture. Above this the suture has become united, and the lines ascend in conformity to the general pattern. It is therefore indicated that lines turning toward the suture are somehow related to that suture, either because of the direction of bone growth, local stresses at the suture, or some other cause.

It is possible that preparation of the inside of the skull vault might reveal relevant information on these problems of deviation from simple muscle-response pattern, but this could not be done on these specimens.

The lines in the gorilla brow ridge deviate more and more toward the side as the region adjacent to the temporal muscle is approached. It is suggested that the area is coming more and more under the influence of the encroaching temporal muscle during the growth of the individual. Eventually the temporal muscle reaches the midline in many gorillas.

It seems possible that the brow ridge area is in transition in its split-line patterns, and that in the adult animal the split-lines would have been continuously horizontal across the brow ridges, as in the chimpanzee. The adult skulls in the two species are very similar in form. The possible rearrangement suggested emphasizes one of the many potentialities of the use of split-line analysis of growth patterns in primates. This is a line of investigation that has only begun to be utilized.

The exterior of the zygomatic arch in the orang utan shows very few organized split-lines on either side. In all other animals processed this area has yielded highly organized splits, yet the lack of splits was predicted before decalcification. The bone here was rough and slightly pitted, resembling unorganized bone frequently found at the human brow ridge and mental protuberance. On the internal face of the arch, however, the split-lines are well defined, paralleling the axis of the arch. The organization of the deeper layers cannot be determined on this specimen, since it is on loan and must be returned.

The close-up picture of the pterygoid and maxillary tuber regions of the orang utan (figure 6) is very revealing as to the relationships between the split-lines, chewing pressures and the pull of the chewing muscles. The lines progressing backward in the maxillary tuber cross over toward the pterygoid process of the sphenoid bone above the third molar. The bone encasing the maxillary sinus here is thicker than it is both above and below. Lines are continuous with these in the pterygoid process of the sphenoid bone, indicating a functional reality for the pterygoid pillar (Weinmann and Sicher, '47). This probably represents a response to the compressive force from the molar teeth. Immediately behind, however, these lines loop back and down in the lateral pterygoid plate, almost certainly in response to the downward pull of the internal pterygoid muscle which originates along its internal face. Those lines which continue upward above this are then turned posteriorly and laterally in the infratemporal fossa, probably under the influence of the external pterygoid muscle originating in this area. Just anterior to this, lines which have ascended in the infratemporal surface of the maxilla deviate backward to end at the infratemporal crest. These also are probably responding to the pull of this muscle. These lines are at right angles to the lines associated with the temporal muscle immediately above. If these interpretations are correct, a number of different forces are analyzed into the areas they predominantly influence.

The pattern at the central portion of the mandible (figure 4)

resembles that reported for man by Seipel ('48) most closely in the orang utan. The split-lines at the base continue from one side to the other, while those closer to the lower incisor teeth generally ascend. In the gorilla the lines coming in from the body of the mandible converge on each side and do not cross the midline. Ascending lines begin at the very base of the symphyseal region. In the gibbon the lines which cross over predominate.

In human beings with well-developed mental protuberances Seipel ('48) found that the bone yielded no definite split-line patterns. He explained this as being the result of the meeting of trajectorial systems at this region. When the surface bone was dissected away, however, he found the regular pattern of lines going across the midline at deeper levels.

None of the specimens processed here shows such a pattern. Other regions of the skull show definite areas where different split-line systems meet without disorganization of the bone. Unorganized bone can be next to bone with well-developed split-lines where a simple stress pattern is indicated. It therefore seems probable that the piling on of unorganized bone has some other explanation than one related to responses to mechanical stress.

It is interesting to note that Henckel ('31) made split-line preparations on the lower jaw of a gibbon, an orang utan and a different species of *Semnopithecus*. He found that the external symphysis region in these forms had split-lines running vertically rather than from one side to the other. He related this difference from man to the difference of the angles at which the mandibular halves come together at the midline. It will be noted that all three of these forms in the present series have basically the same pattern as man. Henckel apparently found a pattern which is highly variable rather than diagnostic.

In the orang utan and gorilla the lines from the incisor and canine teeth ascend into the nasal cavity or parallel its lateral borders to ascend to the brow region between the orbits. In the orang utan they die out just above the fronto-nasal suture, but in the gorilla they continue back on the frontal bone after being deviated somewhat to the right at the top of the developing brow ridge. The divided orang utan brow ridges have no decided split-line patterns, and usually the punctures do not form splits at all. Immediately posterior is a narrow transverse split-line pattern, which is succeeded by lines coursing backward between the superior temporal lines. These continue back to the nuchal area, where



lines continue downward toward the foramen magnum. This region is invaded by the lines along the side of the braincase only as the nuchal area is approached. In the gorilla the lines continue back only as far as the frontal bone extends. Laterally they seem to be deviated by the pull of the temporal muscle, while the split-lines are quite irregular toward the midline. Behind the frontal bone the lines associated with the pull of the temporal muscle continue across to the midline.

Some interpretation of these patterns can be given, but so much remains a problem that the crudity of split-line studies in their present state is emphasized. The patternless state of the small orang utan brow ridges indicates that their formation has little to do with facial stresses, as in man. Here there is a distinct forehead in the same general plane as the face. The meaning of the split-lines coursing backward is not clear to the writer. Is it from chewing pressures, from the pull of nuchal musculature, or a pattern not related to mechanical stresses? The lines just behind the brow ridges extending laterally would indicate tension in that direction, and favor a tensile explanation. However, the backward direction of the lines in the gorilla frontal bone probably represents a continuation of pressures. Certainly there is no continuation to the nuchal area. The great need for developing instrumental tests of the strains taking place in the bone of living animals during normal functioning is particularly revealed by these dubious areas. Electric strain gages have been used by Evans ('53) for this purpose in the tibia of a dog, but the usefulness of the instrument, in biology is yet to be fully realized.

The orang utan resembles the chimpanzee in the infraorbital and zygomatic regions, while the gorilla and gibbon have the laterally-directed patterns found in man. Ascending split-lines in the face of the gibbon do not appear to reach the interorbital region. The lines in the posterior part of the maxilla parallel the alveolar border.

Comments on the remaining primates must be confined to a few general considerations. On the brow ridges, the macaque appears to resemble the chimpanzee closely (figure 5A), with a large continuous brow ridge set somewhat apart from the braincase and the split-lines running continuously in it. In the langur (*Semnopithecus*), however, the supraorbitals are small, divided, and lacking any pattern of lines. Instead, the stress from the chewing muscles must be taken up behind in the frontal bone, if the continuous coronal split-line pattern is any indication. The macaque, on the other hand, has no organized patterns

behind the brow ridge. It is thus apparent that the supraorbital region is very different in some aspects of its functioning in the two forms, as is also the case in the chimpanzee-human comparisons. These different patterns of organization indicate that experimental work on different primates can give answers to many of the problems of the relationship of the supraorbital area to other regions and of the functions of that area in general.

The lemur also has no split-lines in the interorbital region in the frontal bone, except very close to the orbits. The spider monkey has light, divided brow ridges and a considerable forehead, but the supra-orbital region has organized split-lines.

The lateral view of these specimens (figure 5B) shows rather vividly the continuation of lines of the lemur zygomatic arch forward on the maxilla. Anterior to this, the pattern dies out. These lines are here regarded as being a response to the pull of the masseter muscle which seems to have a strong antero-posterior direction in its anterior fibers. This may be another, more extreme example of tension systems of split-lines from the muscle overcoming upward pressures. Actually no ascending split-lines are apparent in this region. It may be observed that the gibbon has a somewhat similar system of lines in the maxilla, and that the low ramus of the mandible gives an antero-posterior direction to the masseter muscle. Here once again ascending lines are not apparent behind the canine teeth.

The lines in the *Semnopithecus* frontal bone previously mentioned are directed toward the lateral orbital region. Externally, this area has no organized split-lines above the zygomatic bone, the pattern being resumed below the suture. However, figure 7 shows that the pattern continues on the orbital side of the frontal bone in this area. This suggests that the stresses in the region are continuations of the general tension system associated with muscle pull, which are reflected in the bone organization at deeper levels here, but that unorganized bone is piled on laterally as in the zygomatic arch of the orang utan.

The close-range photograph of the spider monkey lower jaw (figure 8) is interesting because its transparency allows one to see how the split-lines on opposite sides of single structures conform to each other in some places and deviate in others. The fainter lines paralleling the mandibular notch are on the lateral side, while the ascending darker lines which cross them are on the side facing the viewer. Farther back on the ramus the lateral and medial lines coincide closely. However, the

deviant pattern between the angle of the jaw and the last molar is apparent. The lines descending toward the inferior border of the mandible in two groups are accompanied by a definite thickening of the bone. These are presumably associated with the insertion of the internal pterygoid muscle. The lines on the lateral surface can be seen through the bone even here. This figure illustrates vividly the precise differential response to closely juxtaposed organizing factors revealed by the split-lines.

The mandible is primarily a stress-bearing organ, and it usually has the most completely organized split-lines in the face. The view (figure 9) of the inside of the symphyseal regions shows that nearly all the specimens have lines running across the midline in the basal region. In those specimens in which there is some degree of anterior protrusion, the lines run forward and upward. This is most noticeable in the lemur, orang utan and macaque. The latter two show nearly all their tooth wear on the incisors, and the bone in this region is very massive in both specimens. It is difficult to avoid the inference that the greatest chewing stresses are up in this region in the two specimens.

Split-line patterns have been found in all mammals investigated to date. Common laboratory animals can thus be used in basic experiments on the nature of the Haversian system organization in bone. One has been attempted by the writer, and others are planned. The differences in external appearances and split-line organization of the surface bone in different areas noted in this study indicate that basic histological studies could yield important information. New techniques to supplement split-line analysis are needed, since this is after all a relatively crude approach. Improvements in the technique itself are a crying need. It is at present very tedious and time-consuming. This small project alone involved several hundred man-hours to prepare. The development of a device to make the splits and administer the color at the same time would help enormously. Injection and corrosion preparations are possible for studies of local areas with the use of new techniques being developed by Dr. Batson of Pennsylvania, and new methods of vital staining are now available to help studies of bone growth.

Variations in split-line patterns in man are gradually being revealed as more specimens are processed. This study gives no idea of the variability of patterns and their relationship to form variation within the species processed. Museums are understandably reluctant to give out specimens which will not be returned intact. Even in this study, the

organization of deeper layers of bone must remain a matter of speculation. The necessity for modern primatologists to obtain their own collections is abundantly clear, since only in this way can they get adequate samples from populations and process them as they see fit.

The relationship between the patterns in the bone and soft tissues such as muscles, ligaments and connective tissue can only be guessed at in these specimens. This points up another great need for primate work, the study of soft parts on the same individual in which the skeleton is studied. When hypotheses as to the soft-tissue situation are set up on the basis of split-line analysis of the bone, they can then be tested on other specimens. Only in this way will the functioning organism be understood as anything more than a jumble of unrelated parts.

The variations in form and split-line patterns between the primates processed in this study are quite striking, as the figures reveal. It is also possible to offer plausible functional explanations of some of them. With the further development and application of the method, it should be possible to apply it to problems of the form of fossil primates and hominids. The wide variations to be found within the order offer functional situations very similar to variations in living races and those indicated in fossil man. For example, in this sample there are projecting malar regions similar to Mongoloids (Hooton, '46), and backward-shelving ones similar to Neanderthal man (Howell, '51). When enough such situations have been analyzed, it may be possible to generalize about the relationships of the region to other parts of the skull and to the functional muscle-bone systems implied by them. If a partial genetic analysis is made possible by the technique, taxonomic connections may be traceable with greater certainty, and the processes involved during human evolution should be understood with much greater clarity.

The establishment of functional systems offers possibilities for the genetic analysis of form in primates and man. Where the relationships between different parts of the skull suggested by the split-line patterns are tested by experimental work, the number of genes implied in the determination of form is greatly reduced. This is because the interrelationship implies a single process operating to influence the various parts affected.

Functional analysis with split-lines may be a further aid in the genetics of form. Those structures which have no definite patterns can in all likelihood be said to be unmodified by mechanical stresses, one of

the environmental factors complicating genetic analysis. Others which have a split-line structure, such as the infraorbital bar, can probably be evaluated by experiments as to the extent to which they are a response to stresses or are independently genetically determined.

The previous discussion has indicated how the split-line technique may help to disentangle the primary genetic and the secondary functional causes of form in various regions of the skull by comparisons of different primates, and how this may apply to the interpretation of the variations to be found in man, both living and fossil. The potential uses of non-human primates for these purposes have scarcely been realized, however, going far beyond the limitations of the technique described here. At the very foundation of this potential is the previously unrealized possibility of expanding the scope of human genetics tremendously through the experimental breeding of non-human primates. It seems highly probable that a great many human genes can be elucidated through their homologues in other primates. And since there are many living primates which are pre-adapted for the dramatic steps assumed in human evolution, it may also be possible to reproduce many of these steps through creation and selection of mutations and selection of favorable gene combinations in breeding experiments. It may thus be possible to isolate the actual genetic changes involved in the development of such features as stereoscopic vision, development of brachiating habits, assumption of upright posture, loss of inherited behavioral traits, speech, and the general potentialities for symbolic learning and cultural behavior. This would be important in developing a truly genetic primate taxonomy and in interpreting the fossil and archeological record. More important, however, would be the revelations of the functioning genetic systems in human beings, reflected back by discovery of the processes that were probably involved in their development. At a somewhat less pretentious level, it should be possible to use primate genetics in combination with split-line experiments in further clarifying the relationship between the form and functioning of the minute architecture and gross morphology of the human skeleton.



## LITERATURE CITED

- AHRENS, H. J. 1936 Die Entwicklung der Spaltlinienarchitektur des knöchernen menschlichen Schädels. *Morphol. Jahrb.*, 77: 357-371.
- BENNINGHOFF, A. 1925 Spaltlinien am Knochen, eine Methode zur Ermittlung der Architektur platter Knochen. *Anat. Anz. (Ergänz. heft)*, 60: 189-206.
- 1927 Über die Anpassung der Knochenkompakta an geänderte Beanspruchung. *Anat. Anz.*, 63: 289-299.
- EVANS, F. G. 1953 Methods of studying the biomechanical significance of bone form. *Am. J. Phys. Anthropol.*, n. s. 11: 413-435.
- HENCKEL, K. O. 1931 Vergleichend-anatomische Untersuchungen über die Struktur der Knochenkompakta nach der Spaltlinien-methode. *Morphol. Jahrb.*, 66: 22-45.
- HOOTON, E. A. 1946 *Up From the Ape*. 2nd edition. Macmillan, New York.
- HOWELL, F. C. 1951 The place of Neanderthal man in human evolution. *Am. J. Phys. Anthropol.*, n. s. 9: 379-416.
- MURRAY, P. D. F. 1936 *Bones; a study of the development and structure of the vertebrate skeleton*. Cambridge University Press, Cambridge.
- SEIPEL, O. M. 1948 Trajectories of the jaws. *Acta Odontologica Scandinavica*, 8: 81-191.
- TAPPEN, N. C. 1953 A functional analysis of the facial skeleton with split-line technique. *Am. J. Phys. Anthropol.*, n. s. 11: 503-532.
- WEINMANN, J. P. AND H. SICHER 1947 *Bone and Bones*. C. V. Mosby, St. Louis.





# METRIC AND MORPHOLOGIC VARIATIONS IN THE DENTITION OF THE LIBERIAN CHIMPANZEE; COMPARISONS WITH ANTHROPOID AND HUMAN DENTITIONS

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THE largest known collection of chimpanzee crania and calvaria (291 in all) from a single area, northeastern Liberia, provides an unusual opportunity to study in detail the dentition of the chimpanzee. Dr. George W. Harley of Ganda, Liberia, secured the collection for the Peabody Museum, Harvard University, and in turn it was made available to us by Dr. Earnest A. Hooton for our studies on the dentition. Investigations have been conducted of both the macrostructure (metric and morphologic details) and the microstructure of chimpanzee teeth. The latter has been described in a preliminary report (Schuman and Sognaes, '52). This paper is an assessment and evaluation of the metric and morphologic variations of chimpanzee dentition.

Part I (Metric) consists of a recording of dimensions: their means, ranges, standard deviations, coefficients of variation, modules, indices (talonid-trigonid, length-breadth). These data are compared to similar data of anthropoid and human dentitions.

Part II (Morphology) lists observations on mandibular molar patterns and the hypocone and cingulum of maxillary molars. Comparisons are made to similar observations from human groups.

## PART I

### METHODS

*Mesial-Distal Diameter:* (Length) In molars this measurement is taken between the mesial and distal contact points and on an axis mid-way between the buccal and lingual surfaces. In incisors, this measurement is taken as the maximum between mesial and distal contact points and is referred to as "width."

*Buccal-Lingual Diameter:* (Breadth) It is the maximum buccal-lingual diameter on an axis perpendicular to the plane used for the mesial-distal measurement.

*Cervical-Incisal Diameter:* (Height) This measurement is taken on the labial surface as nearly parallel to the vertical median crown axis as possible from incisal tip to lowest cervical point of enamel.

*Talonid-Trigonid Diameters:* These are breadth diameters in the mandibular molars of the posterior and anterior moieties respectively. Each is measured at the maximum breadth irrespective of the perpendicular to the length plane. The trigone is slightly wider than the usual maximum breadth (described above) except in mandibular  $M_1$  where the talone is the broader measurement.

Mesial-distal and buccal-lingual measurements of the maxillary and mandibular molars, the maxillary premolars, and the mandibular second premolars were taken. Measurement of the mandibular first premolar were omitted, since this tooth is so skewed and variable in form as to make repeated accurate measurements unfeasible. Also, the mandibular first premolars in human dentitions are not comparable to those of the anthropoid apes.

The mesial-distal diameter in the case of the canine is unlike that taken of the molars and premolars. In chimpanzee canines, the maximum mesial and distal points are found close to the cervix of the crown; in human canines, this maximum diameter is nearer the incisal tip.

Incisors have been measured only in the mesial-distal diameter. Cervical-incisal diameters were not available in sufficiently large samples due to the fact that usually all incisors had undergone attrition to a point where accurate measurement of the height of the crown was not feasible.

In general, the methods of measurement described are similar to those utilized by investigators whose data are compared with ours. All measurements were taken with the Boley gauge, which is a small sliding caliper, calibrated to 0.1 mm and used chiefly by orthodontists. For our purpose, the gauge was modified by grinding the beaks fine, so as to produce measurements of greater accuracy.

Repeated measurements on the same teeth at various times produced an average error of 0.2 mm. This compares favorably with that of Pedersen ('49) who states that on repeated measurements by the same person, the difference was at most not more than 0.2 mm. Nelson ('38), on the other hand, maintains that a metrical accuracy of 0.1 is easily attained in mesio-distal and labial-lingual dimensions but that an accuracy of greater than 0.3 mm cannot be obtained for crown height. However, Nelson does not make clear whether this degree of error

was arrived at after testing repeated measurements on the same teeth. Less optimistic is Shaw ('31) who says that it is impossible to obtain accuracy better than 0.5 mm.

Measurements were made only on teeth in which the degree of attrition had not altered the original dimensions.

In general, teeth on the right side were selected for measurement. Where intact groups of teeth were not available on the right side, teeth from the left side were measured. This did not affect the results, since in testing it was found that there was no significant difference between right and left measurements. Ashton and Zuckerman ('50) also found no significant difference between right and left teeth.

#### METRIC DATA OF LIBERIAN CHIMPANZEE DENTITION

Table 1 contains the metric data of the maxillary and mandibular molars and premolars (mandibular first premolar excluded) of the Liberian chimpanzee. The symbols  $M_1$ ,  $M_2$ ,  $M_3$  refer to first, second and third molars respectively.  $PM_1$  and  $PM_2$  refer to first premolar and second premolar. The values for female and male specimens are listed separately, as are their combined values. All female mean dimensions are smaller than male. These mean differences were tested for significance according to Snedecor's formula ('50, p. 81). The breadth diameters of male maxillary molars, maxillary premolars, and mandibular  $M_3$  are significantly greater than those of the female. In mandibular  $M_1$ ,  $M_2$ ,  $PM_2$  the breadth diameters of the male approach borderline significance over those of the female. It would seem therefore that all the male molars and premolars tend to be significantly broader than those of the female. Significance in length diameters favoring the male were found only in three of 9 teeth: maxillary  $M_2$ ,  $M_3$ , mandibular  $M_1$ , none of the premolars exhibiting this significance. None of the female length diameters were significantly greater than those of the male. Ashton and Zuckerman ('50, p. 472) in their measurements of orangutan, gorilla and chimpanzee dentitions found that "in all the dimensions which are not affected by attrition, every male tooth is larger than the corresponding female tooth."

In table 1, the mesial-distal (length) diameters diminish proceeding from maxillary  $M_1$  to  $M_3$ , and from maxillary  $PM_1$  to  $PM_2$ . If the means of the buccal-lingual (breadth) diameters are corrected to one place<sup>1</sup> (as they are for comparisons to other groups),  $M_1$  and  $M_2$  do

<sup>1</sup> Two decimal places have been maintained for the record, but are of little practical value, since the measurements themselves were taken to 0.1 mm and the average measurement error is 0.1 mm.

TABLE 1  
Dimensions and Variations in Liberian Chimpanzee Dentition

MAXILLARY TEETH											
Mesial-Distal						Buccal-Lingual					
	N	Range	Mean	S. D.	C. V.	N	Range	Mean	S. D.	C. V.	Module
M <sub>1</sub>	Total	226	9.0-12.6	10.70	0.54	225	9.9-12.7	11.57	0.48	4.1	11.13
	♂	132	9.0-12.3	10.73	0.58	132	10.6-12.7	11.66	0.48	4.1	11.19
	♀	94	9.5-11.8	10.66	0.47	93	9.9-12.6	11.46	0.48	4.2	11.06
M <sub>2</sub>	Total	229	8.7-11.9	10.25	0.59	228	10.0-13.6	11.62	0.59	5.1	10.93
	♂	132	9.0-11.9	10.37	0.60	131	10.5-13.6	11.76	0.64	5.4	11.06
	♀	97	8.7-11.9	10.12	0.58	97	10.0-12.6	11.44	0.57	5.0	10.78
M <sub>3</sub>	Total	208	7.3-11.8	9.34	0.69	209	9.2-13.2	10.86	0.64	5.9	10.11
	♂	120	7.3-11.8	9.55	0.69	121	9.3-13.2	10.90	0.64	5.9	10.22
	♀	88	7.7-11.7	9.10	0.70	89	9.2-12.1	10.67	0.64	6.0	9.83
PPM <sub>1</sub>	Total	219	6.7-10.1	8.38	0.58	216	8.3-11.8	10.21	0.59	5.8	9.29
	♂	125	6.7-10.1	8.42	0.59	122	8.9-11.8	10.35	0.55	5.3	9.39
	♀	94	7.2-10.0	8.33	0.58	94	8.3-11.4	10.07	0.64	6.4	9.20
PPM <sub>2</sub>	Total	197	6.0-9.8	7.50	0.59	194	7.3-12.2	10.27	0.58	5.6	8.88
	♂	115	6.0-9.8	7.57	0.65	112	7.3-12.2	10.39	0.62	6.0	8.98
	♀	82	6.1-8.4	7.44	0.49	82	8.9-11.5	10.15	0.53	5.2	8.78
MANDIBULAR TEETH											
M <sub>1</sub>	Total	128	9.9-13.2	11.24	0.50	128	9.2-12.0	10.35	0.52	5.0	10.79
	♂	64	10.4-13.2	11.36	0.51	64	9.3-12.0	10.47	0.50	4.8	10.92
	♀	64	9.9-12.2	11.12	0.49	64	9.2-11.8	10.24	0.54	5.3	10.68
M <sub>2</sub>	Total	128	9.9-13.0	11.11	0.59	126	9.5-12.6	10.98	0.51	4.7	11.04
	♂	65	9.9-13.0	11.20	0.63	64	9.9-12.6	11.07	0.50	4.5	11.13
	♀	63	9.2-12.8	11.01	0.55	62	9.5-12.5	10.91	0.52	4.8	10.96
M <sub>3</sub>	Total	117	9.2-12.4	10.50	0.63	117	8.8-12.1	10.38	0.55	5.3	10.40
	♂	61	9.2-12.4	10.54	0.65	61	9.6-12.1	10.58	0.57	5.4	10.56
	♀	56	9.3-11.8	10.46	0.61	56	8.8-11.3	10.22	0.53	5.2	10.34
PM <sub>2</sub>	Total	128	7.0-10.0	8.24	0.54	128	7.3-11.1	9.04	0.62	6.9	8.59
	♂	65	7.0-10.0	8.31	0.61	65	7.5-11.1	9.15	0.67	7.3	8.73
	♀	63	7.0-9.6	8.17	0.47	63	7.3-10.6	8.92	0.58	6.5	8.54

C.V. =  $\frac{S.D. \times 100}{\text{Mean}}$ 
Module =  $\frac{\text{Length} + \text{Breadth}}{2}$ 
Length = Mesial Distal, Breadth = Buccal Lingual.

C. V. = S. D. X 100.    Module =  $\frac{\text{Length} + \text{Breadth}}{2}$     Length = Mesial Distal. Breadth = Buccal Lingual.



not differ in breadth, but  $M_3$  is significantly less broad. The premolars do not differ in breadth.

The length of mandibular  $M_1$  is slightly greater than  $M_2$  and significantly greater than  $M_3$ . The breadth of  $M_2$  is significantly greater than  $M_1$  and  $M_3$  which nearly equal each other in this diameter. This greater breadth of  $M_2$  is the only dimensional feature manifested in chimpanzee molars that is reminiscent of the fossil and modern anthropoid characteristic of increased dimensions from  $M_1$  to  $M_2$  and  $M_3$ .

An examination of the coefficients of variation discloses  $M_1$  as the least variable, and  $M_3$  as most variable in the maxillary and mandibular molar classes respectively. Also, maxillary  $PM_2$  is more variable than  $PM_1$ . These data are consistent with the findings of Dahlberg ('45) who applied Butler's ('39) "field" theory to the dentition. The following illustration from Dahlberg ('49, p. 139) will aid in understanding the concept. The symbol  $S$  denotes the tooth in each group

	S	V	S	S	V	S	V	V
Maxillary	$I_1$	$I_2$	C	$PM_1$	$PM_2$	$M_1$	$M_2$	$M_3$
Mandibular	$I_1$	$I_2$	C	$PM_1$	$PM_2$	$M_1$	$M_2$	$M_3$
	V	S	S	S	V	S	V	V

that is morphologically more stable in the expression and retention of ancestral patterns and the resistance to anomalous impositions. The other teeth in the respective tooth groups, indicated by the symbol  $V$ , are more variable. The greater the distance from the polar, or stable tooth, in a "field," the greater the variability. Dahlberg ('45) has indicated the validity of this theory in connection with the morphological features of human teeth.

To this theory is now added the support of metric data of the chimpanzee dentition. Figure 1 graphically illustrates the mean dimensions with their coefficients of variation in the molar and premolar teeth of Liberian chimpanzees. In general, length dimensions are more variable proceeding from  $M_1$  to  $M_3$  in both maxilla and mandible. A similar increase in the variability of the breadth diameters is noted in the maxilla from  $M_1$  to  $M_3$ . An inconsistency with the "field" concept may be present in the coefficients of variation of the breadth diameters in mandibular  $M_1$  and  $M_2$ , where the latter is slightly less variable. However, differences in variability of breadth diameters in mandibular molars from  $M_1$  to  $M_3$  are slight. The low coefficient of variation in mandibular  $M_2$  may represent a persistence of the anthropoidal characteristic of the greater breadth of this tooth. Another inconsistency to the concept of

variability is seen in the maxillary premolars, in which the breadth diameter of  $PM_1$  is slightly more variable than that of  $PM_2$ , although the length of  $PM_2$  is markedly more variable than  $PM_1$ .

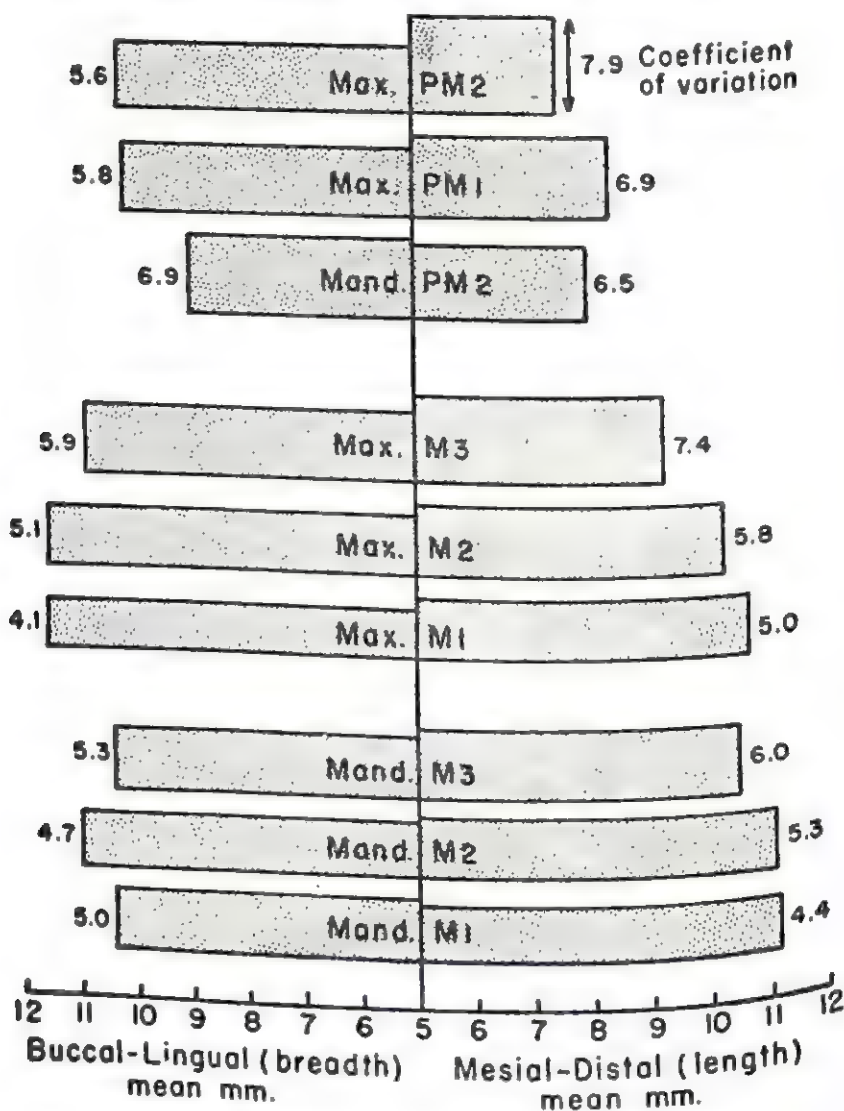


FIG. 1. MEAN DIMENSIONS AND COEFFICIENTS OF VARIATION OF LIBERIAN CHIMPANZEE TEETH.

It is generally agreed that the central tendencies indicated by mean values often obscure the variabilities around the means. For example,

it has just been demonstrated that the trend of the mean values is a decrease in dimensions from  $M_1$  to  $M_3$ . However, there are many exceptions to this generality when the sequence within each molar group is noted. Table 2 lists these sequential variations. Neither the anthropoid progression  $M_1 < M_2 < M_3$  nor the hominid regression  $M_1 > M_2 > M_3$  alone predominates in a majority of the molar series. Several variations of both formulae appear in appreciable percentages. For example,  $(M_1M_2)M_3$  and  $M_2M_1M_3$  are almost equal in occurrence with  $M_1M_2M_3$ . Noteworthy are the relatively high percentages of  $M_2(M_1M_3)$  and  $M_2M_3M_1$  in the buccal-lingual diameters of mandibular molars of both male and female.

#### COMPARATIVE METRIC DATA

Senyurek's ('39) data on the orangutan and gorilla dentitions are selected for comparisons because of their completeness. Hrdlička ('26) published measurements of only the mandibular  $M_1$  and  $M_2$  of orangutan, gorilla and chimpanzee. Ashton and Zuckerman measured the dentitions of orangutan, gorilla and chimpanzee, but combined the dimensions of the unworn molars and premolars with those having undergone considerable attrition, so that the original tooth dimensions are obscured ('50). Gregory and Hellman ('26) confined their measurements to the mandibular molars and premolars, giving the mesial-distal and trigonid values.

Pedersen's data on East Greenland Eskimos ('49, pp. 80-81) and those of Nelson ('38, pp. 265-266) on the Pecos Indians are included for two reasons:

1. Both investigators have provided more statistically treated data than have most.
2. Pecos Indians and East Greenland Eskimos are similar to the Liberian chimpanzee in their homogeneity—having shared a common environment in relative isolation.

Pedersen provided sufficient data to permit our computing the coefficients of variation. In these computations, the values of right and left teeth were combined. The validity of this procedure has been previously stated (p. 241).

Nelson was forced to use samples sorted from loose teeth, so that sex groupings were not possible. In making our comparisons, we should consider Nelson's ('38, p. 278) statement to the effect that Pecos tooth dimensions are in the intermediate range of human populations. Campbell's data on the Australian Aboriginal dentition ('25, p. 17) are included because of their place at the top of the range of human teeth. Stein ('34, p. 1411) measured larger samples of American Whites than did G. V. Black. The latter did not indicate the size of his samples, but simply stated that a sufficient number of each variety of teeth were measured ('02, p. 14). Senyurek's *Homo sapiens* group provides dimensions on premolars and ranges of molars which have been omitted by Stein. Although Senyurek does not so state, it is implied that *Homo sapiens* refers to a group

TABLE 2  
Dimensional Variations in the Sequence of Liberian Chimpanzee Teeth  
(in terms of percentages)

	MAXILLARY			MANDIBULAR		
	Mesial-Distal	Buccal-Lingual		Mesial-Distal	Buccal-Lingual	
*M <sub>1</sub> M <sub>2</sub> M <sub>3</sub>	♂ 48	♀ 71	♂ 18	♀ 20	♂ 9	♀ 9
(M <sub>1</sub> M <sub>2</sub> ) M <sub>3</sub>	19	20	35	40	25	21
M <sub>2</sub> M <sub>1</sub> M <sub>3</sub>	9	2	23	16	23	16
M <sub>2</sub> (M <sub>1</sub> M <sub>3</sub> )	3	0	9	10	21	9
M <sub>1</sub> (M <sub>2</sub> M <sub>3</sub> )	9	3	6	5	4	36
(M <sub>1</sub> M <sub>2</sub> ) M <sub>3</sub>	5	2	6	6	7	0
M <sub>2</sub> M <sub>3</sub> M <sub>1</sub>	2	0	1	0	14	7
(M <sub>2</sub> M <sub>3</sub> ) M <sub>1</sub>	1	1	2	2	25	16
No. of Molar					9	9
Groups Measured	110	85	107	82	57	56

Four additional variations in sequence were encountered, in remaining small percentages:

$$\begin{array}{c} M_1 M_2 M_3 \\ M_2 M_3 M_1 \\ (M_1 M_3) M_2 \\ M_3 M_1 M_2 \end{array}$$

\* M<sub>1</sub> M<sub>2</sub> M<sub>3</sub> is the basic formula, indicating that M<sub>1</sub> is greater than M<sub>2</sub>, M<sub>2</sub> greater than M<sub>3</sub>. Order of dimension decrease reads from left to right in all formulae. Two or more teeth in parenthesis denote equal dimension. Since the error of measurement is 0.2 mm and each measurement is taken to 0.1 mm, differences in sequence in table 2 were recorded only when of the order of 0.3 mm or more. Any two diameters with a difference of 0.2 mm or less were considered as equal.

limited to White individuals. Senyurek's and Stein's data are similar to the values published by G. V. Black, and all of these are in the lower or lowest rank order of human tooth dimensions.

Due to the limitation of space, most comparative data are illustrated in graphs and figures, rather than recorded in tables. Figure 2 graphically summarizes the comparative dimensions of the molars and premolars of Liberian chimpanzee, orangutan, and human groups. The

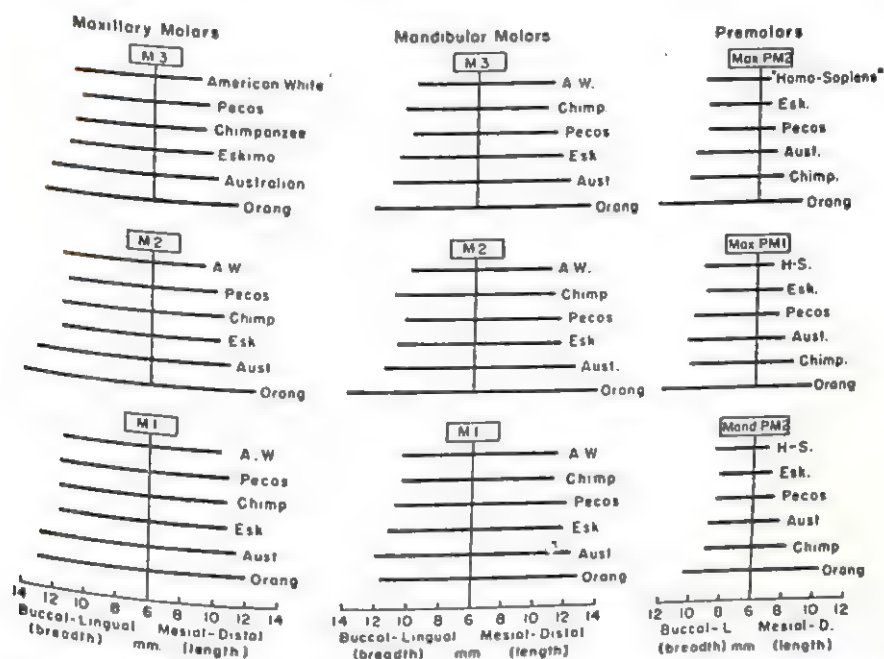


FIG. 2. MEAN DIMENSIONS OF CHIMPANZEE MOLARS AND PREMOLARS COMPARED TO THOSE OF ORANGUTAN AND HUMAN GROUPS

lines indicating mean values for breadth (on left) and length (on right) are arranged in rank order according to modules. The crown module is  $\frac{\text{Length} + \text{Breadth}}{2}$ . Pedersen, Hrdlička, Shaw, Nelson, and others agree

that the crown module is an "expression of mass size" of the crown, although Pedersen ('49, p. 79) terms this a rather imperfect device. However, the crown module does give some indication of "relative" overall size rather than mass. It is quickly evident that the chimpanzee



molar mean dimensions fall well within human values, although their rank order differs slightly in mandibular and maxillary arrangement. The Liberian chimpanzee premolars suggest a central tendency just outside that of human premolars, although considerably closer to Australian than to orangutan.

Figure 3 is a graphic representation of the extent of the ranges of anthropoid and human molar dimensions. The comparisons are confined to maxillary  $M_1$  and mandibular  $M_1$  because these are the most stable molar teeth and would therefore be least likely to overlap in ranges among the various groups. Despite this, range values of the molars of Liberian chimpanzee, human groups, and orangutan consistently overlap with each other. In one case, the range of the buccal-lingual dimension of Australian mandibular  $M_1$  is well within the gorilla range. The cross bars (figure 3) bisecting the vertical "range" lines represent mean values of dimensions.

In figure 4 the chimpanzee maxillary premolar alliance with human premolars is emphasized in the range values, which readily overlap. Also, the upper ranges of chimpanzee premolars overlap with orangutan ranges. Of added significance is the fact that overlap of ranges occurs even though there is great disparity in the sizes of the samples compared.

Most investigators compute the Length-Breadth Index of molars:  $\frac{\text{Breadth} \times 100}{\text{Length}}$ . This index is intended to disclose a general "shape" of the tooth and to provide a comparison of these "shapes" among various groups. Some fairly consistent generalizations may be derived from these indices.<sup>2</sup> Upper molar breadth exceeds length, and the index is therefore of a value above 100. From  $M_1$  to  $M_3$  this index increases in orangutan, chimpanzee and human groups. The index of gorilla, however, is practically unchanged from  $M_1$  to  $M_3$ . In mandibular molars, the index is generally below 100 (gorilla has the smallest mean index, 86% in  $M_1$ , Senyurek, '39), but a progression (or regression) of the index is absent in lower molars except for a slight tendency toward increase in  $M_2$  in most groups. Senyurek (p. 121) states, "There is considerable variation in crown indices of the molars of anthropoids and the fact that the ranges of anthropoid indices overlap those of Hominid makes it impossible to use the crown index as a diagnostic criterion in classification of fossil [or other] specimen." The indices of

<sup>2</sup> The values of the indices discussed are taken from Senyurek's tables ('39, p. 112, p. 137).

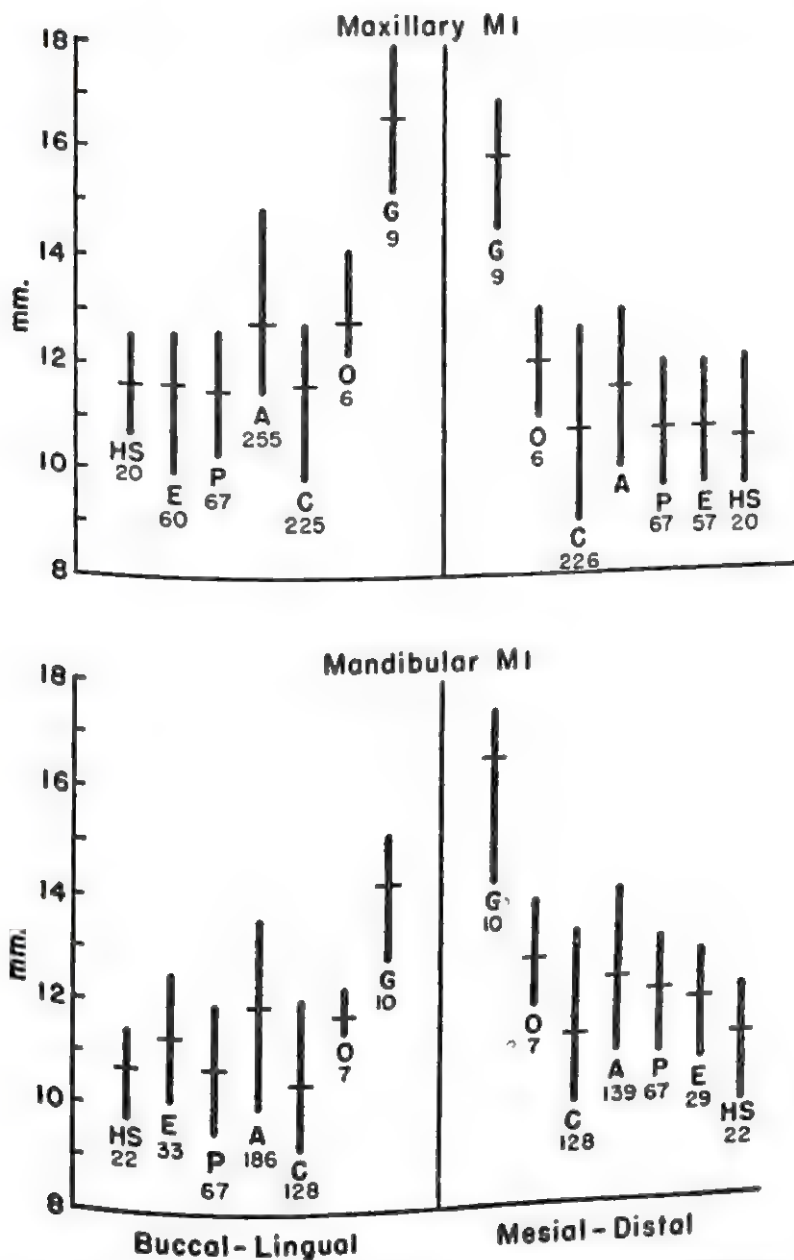


FIG. 3. RANGES OF DIMENSIONS OF FIRST MOLARS IN ANTHROPOID AND HUMAN GROUPS.

Vertical lines indicate extent of ranges.

Cross bars indicate mean values.

Numerals at bottom of each range indicates size of sample.

C = Chimpanzee (Liberian)

E = Eskimo (Pedersen)

P = Pecos Indians (Nelson)

A = Australian (Campbell)

O = Orangutan (Senyurek)

G = Gorilla (Senyurek)

HS = *Homo sapiens* (Senyurek)

*Homo sapiens* group included here in place of American Whites (figure 2) because ranges of latter not available.

the molars of Liberian chimpanzee are similar to the others just described and are therefore not tabulated or illustrated.

Since length and breadth indices do not seem to disclose differences between anthropoid and human molars, we suggest the use of another

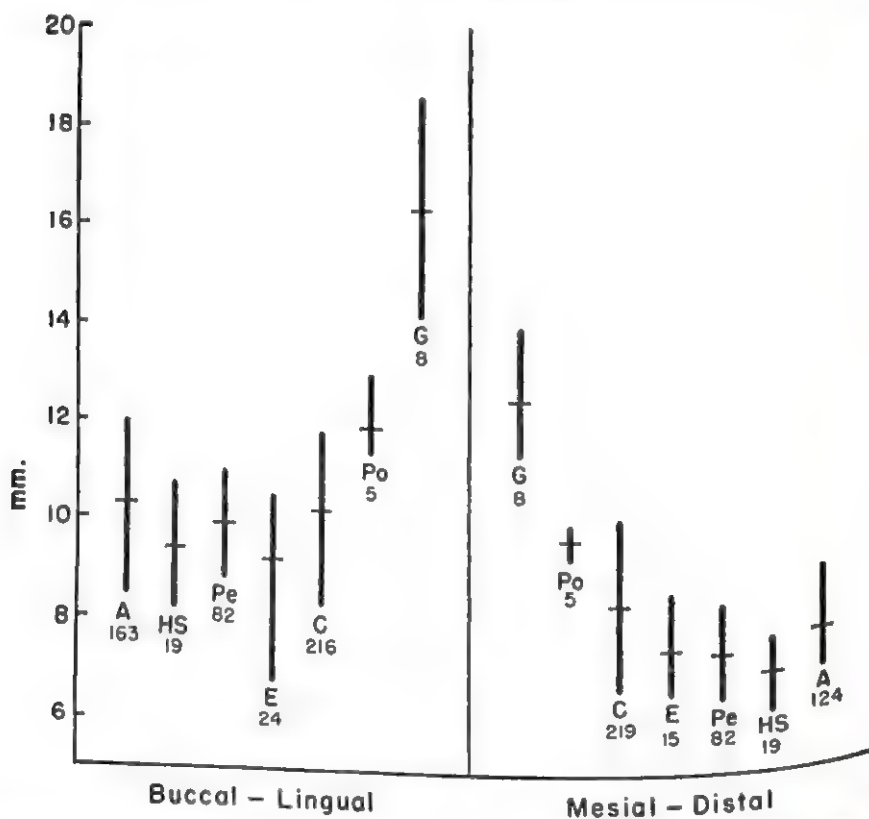


FIG. 4. RANGES OF DIMENSION OF MAXILLARY FIRST PREMOLARS IN ANTHROPOID AND HUMAN GROUPS.

Vertical lines indicate extent of ranges.

Cross bars indicate mean values.

Numerals at bottom of each range indicates size of sample.

Note: In this figure Po = orangutan (Senyurek) and Pe = Pecos Indians (Nelson).

device for comparing the changing "shapes" of teeth and the processes by which such changes are accomplished. This is utilized in table 3, where proportional changes in the dimensions of maxillary and mandibular  $M_2$  and  $M_3$  are expressed as percentages of the dimensions of the respective  $M_1$  teeth. In this tabulation, the chimpanzee  $M_2$  and  $M_3$

TABLE 3  
Decrease or Increase of Dimensions of  $M_2$  and  $M_1$   
(expressed in percentage of maxillary and mandibular  $M_1$  dimensions respectively)

	Gorilla		Orangutan		Chimpanzee		Pecos		Eskimo		American White	
	L	B	L	B	L	B	L	B	L	B	L	B
Maxillary												
$M_2$	+8	+5	+4	+9	-4	+1	-8	-3	-5	-1	-11	+2
$M_1$	-1	-2	-6	+1	-13	-6	-12	-8	-10	-4	-14	-4
Mandibular												
$M_2$	+10	+14	+9	+11	-1	+6	-5	-2	-3	-3	-5	-3
$M_1$	+10	+12	+5	+6	-7	0	-8	-6	-3	-4	-4	-5

L = Length (Mesial-Distal).  
B = Breadth (Buccal-Lingual).

follow more closely the trend of human molars in the percentages of dimensional decreases in terms of  $M_1$ . The one notable exception is an increase in the breadth of the chimpanzee mandibular  $M_2$ , another reminder that this is the only case where a chimpanzee molar dimensionally resembles other anthropoid molars. Gorilla and orangutan are unlike the chimpanzee in that, with the exception of the maxillary  $M_3$ , both dimensions of length and breadth increase from  $M_1$  to  $M_3$ . The maxillary  $M_3$  of gorilla is slightly smaller than its  $M_1$  in both length and breadth. The orangutan maxillary  $M_3$  undergoes appreciable decrease in length compared to  $M_1$  but is about equal to  $M_1$  in breadth. In maxillary  $M_2$  and  $M_3$  of the chimpanzee and human groups, the proportionate decreases are greater in length than in breadth. In the mandibular molars of the human group, the length and breadth modifications nearly keep pace with each other. The mandibular  $M_2$  of the chimpanzee markedly increases in breadth over  $M_1$ , while the length diameters remain about equal. On the other hand,  $M_3$  of the chimpanzee shows a large decrease in length and a stability of breadth with reference to  $M_1$ .

As in the case of length-breadth indices, the talonid-trigonid indices of anthropoids and human groups overlap in their ranges. Nevertheless, the ape molars seem to differ from human molars in the trends of these indices. In figure 5, the talonid-trigonid mean indices of human groups tend toward stability in all three molars, while in all the anthropoid groups these indices markedly decrease from  $M_1$  to  $M_3$ . In other words, the talonid breadth decreases relative to trigonid breadth from  $M_1$  to  $M_3$ . The chimpanzee mandibular molars in this case line up with those of the other anthropoids. In the human groups, the absolute values of mean indices for each of the three molars exceed those of the anthropoids except in the case of chimpanzee  $M_1$ , where the value is of human order. However, more and larger samples of human molars should be measured to determine the validity of the trends described.

Male and female values for Liberian chimpanzee and Eskimo have been combined to give a total coefficient of variation in each case. Over all male and female coefficients of Liberian chimpanzee teeth were tested for significant differences with negative results.

In the three groups compared in table 4, the trend of increasing variability from  $M_1$  to  $M_3$  in both maxilla and mandible, and from  $PM_1$  to  $PM_2$  in maxilla, is almost consistently maintained, reflecting the validity of Butler's field theory. This applies particularly to length



dimensions. Outstanding exceptions are the breadth coefficients in the premolars of all three groups, where there is greater variability in PM<sub>1</sub>. Other inconsistencies are found in the Pecos group. These may be due to the difficulties Nelson encountered in sorting the teeth to be measured. M<sub>1</sub> and M<sub>2</sub> and even an occasional M<sub>3</sub> may have been interchanged. If

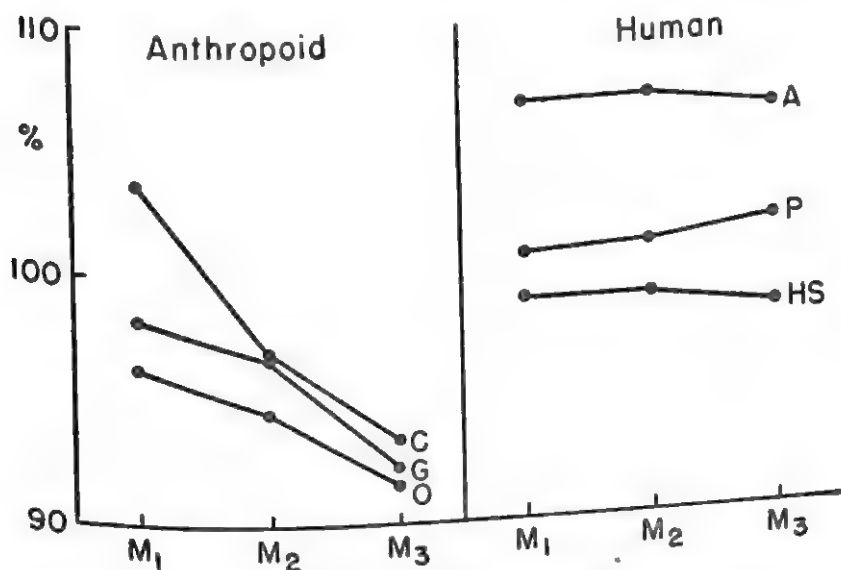


FIG. 5. TRIGONID-TALONID INDICES OF ANTHROPOID AND HUMAN MANDIBULAR MOLARS.

C = Chimpanzee (Liberian)  
G = Gorilla (Senyurek)  
O = Orangutan (Senyurek)

HS = *Homo sapiens* (Senyurek)  
P = Pecos (Nelson)  
A = Australian (Campbell)

The dots indicate mean trigonid-talonid indices:  $\frac{\text{Talonid}}{\text{Trigonid}} \times 100$ .

In anthropoid groups, the trigonid-talonid mean indices decrease from M<sub>1</sub> to M<sub>3</sub>, resulting in increasingly tapered teeth. The trigonid-talonid mean indices in human groups tend toward uniformity from M<sub>1</sub> to M<sub>3</sub>. For each of the three molars, respectively, the absolute mean values of trigonid-talonid indices in human groups exceed those of anthropoids except in the case of chimpanzee M<sub>1</sub>.

this occurred a sufficient number of times, the expected variability trend could have been disturbed. The low coefficient in breadth of chimpanzee mandibular M<sub>2</sub> has been previously commented upon.

In general, the coefficients of maxillary teeth indicate a greater variability as contrasted to the corresponding mandibular teeth. This is more clear cut when the average coefficients are compared within each

TABLE 4  
Coefficients of Variation Compared;  
*Liberian Chimpanzee, East Greenland Eskimo, Pecos Indian*

	$M_1$ *L	$M_2$ L	$M_2$ B	$M_3$ L	$M_3$ B	$PM_1$ L	$PM_1$ B	$PM_2$ L	$PM_2$ B	Av.
MAXILLARY TEETH										
Chimpanzee (Schuman Brace)	5.0	4.1	5.8	5.1	7.9	5.9	6.9	5.8	7.9	5.6
Eskimo (Pedersen)	5.0	4.6	5.1	5.7	8.9	6.8	6.5	6.1	7.6	5.8
Pecos (Nelson)	4.5	3.6	4.8	5.7	6.4	5.4	5.3	5.8	6.8	4.8
MANDIBULAR TEETH										
Chimpanzee	4.4	5.0	5.3	4.7	5.0	6.3	...	...	6.5	6.9
Eskimo	4.1	4.5	4.7	5.6	6.5	6.3	...	...	5.1	5.2
Pecos	4.6	4.4	4.0	4.5	5.9	5.3	...	...	6.2	6.0

\*L = Length; B = Breadth.

of the three groups. Also it is seen that the average coefficient for Liberian chimpanzee molars and premolars (excluding the mandibular first premolar) is of the order of the two human groups, falling between East Greenland Eskimos and Pecos Indians for maxillary teeth and only slightly higher than either in the mandibular teeth. In line with Schreider's discussions ('53, p. 52) on the biometrics of physiology, we tested individual variations with reference to the error of measurement. For example, the smallest coefficient of variation (4.1%) in the Liberian chimpanzee dentition is that of the buccal-lingual diameter of maxillary  $M_1$  (table 1). Since the error of measurement is 0.2 mm, the percentage for the particular diameter (11.6 mm) is 1.7% and therefore does not invalidate the 4.1% coefficient of variation. Similarly, in our remaining data, the percentage errors of measurement do not invalidate the true coefficients of variation.

Data on the chimpanzee canines are recorded in table 5. In spite of the striking differences in the cervical-incisal mean diameters between male and female in maxillary and mandibular canines of the Liberian chimpanzee, the range figures indicate male and female overlapping in both teeth. Therefore, to attempt an assessment of the sex of a chimpanzee skull, on the basis of the height of the canine alone, would often be a very questionable procedure. The sex difference in the mesial-distal diameter is not nearly as marked as the height differences; there is greater overlapping of mesial-distal ranges.

Figure 6 demonstrates that the canines of the chimpanzee are well outside of human range with one exception: the mesial-distal diameter ranges of the mandibular canines of female chimpanzee, Pecos Indians and *Homo sapiens* do overlap.

Table 6 consists of the mesial-distal diameters of Liberian chimpanzee incisors. The "field" concept is apparently adhered to in the maxillary incisors of the Liberian chimpanzee, in which the lateral incisors are the more variable. The mandibular central incisor of the male chimpanzee is also consistent with the expected reversal in variability—central incisor more variable than lateral incisor (see formula, p. 243). However, the female chimpanzee mandibular incisors seem to deviate from the "law" of variability in maintaining a greater variability in the lateral incisors. To offset this exception, it may be pointed out that the question of which mandibular incisor is more variable has never been settled. Additional data should serve to clarify the point.

TABLE 5  
Dimensions and Variations of Canine Teeth  
(Liberian Chimpanzee)

	Cervical Incisal					Mesial Distal					Height Length
	N	Range	Mean	S. D.	C. V.	N	Range	Mean	S. D.	C. V.	
<i>Maxillary</i>											
Total	54	13.8-27.1	19.4	2.3	11.7	97	10.6-16.7	13.1	.93	7.1	147
♂	31	16.1-27.1	22.1	2.3	10.4	51	10.9-16.7	14.3	1.1	7.7	155
♀	23	13.8-18.5	15.9	1.2	7.5	46	10.6-13.2	11.8	.65	5.5	138
<i>Mandibular</i>											
Total	62	13.5-25.0	18.1	1.8	9.9	95	7.5-12.7	10.1	.75	7.4	179
♂	35	14.8-25.0	20.5	2.1	12.4	51	8.5-12.7	11.0	.8	7.3	186
♀	27	13.5-18.3	15.8	1.2	7.6	44	7.5-11.0	8.9	.62	7.0	177

Height = Cervical Incisal.

Length = Mesial Distal.

TABLE 6  
Mesial-Distal Diameters of the Incisors of the Liberian Chimpanzee

Maxillary I <sub>1</sub>						Maxillary I <sub>2</sub>				
No.	Range	Mean	S. D.	C. V.	No.	Range	Mean	S. D.	C. V.	
♂	27	10.2-13.5	12.0	.75	6.3	25	8.5-10.9	9.7	.62	6.4
♀	22	11.1-13.5	12.0	.60	5.0	23	8.1-10.6	9.3	.56	6.0
Total	49	10.2-13.5	12.0	.69	5.8	48	8.1-10.9	9.5	.59	6.2
Mandibular I <sub>1</sub>						Mandibular I <sub>2</sub>				
♂	27	7.1-9.5	8.1	.60	7.4	25	8.0-10.0	9.1	.41	4.5
♀	26	7.3-8.9	8.1	.40	4.9	21	7.9-10.0	8.8	.55	6.3
Total	53	7.1-9.5	8.1	.53	6.5	46	7.9-10.0	9.0	.46	5.1

I<sub>1</sub> = Central Incisor.I<sub>2</sub> = Lateral Incisor.

In figure 7, it is seen that the mean values of mesial-distal diameters of the chimpanzee central incisors are much greater than the corresponding means found in human incisors. Also, the mesial-distal ranges

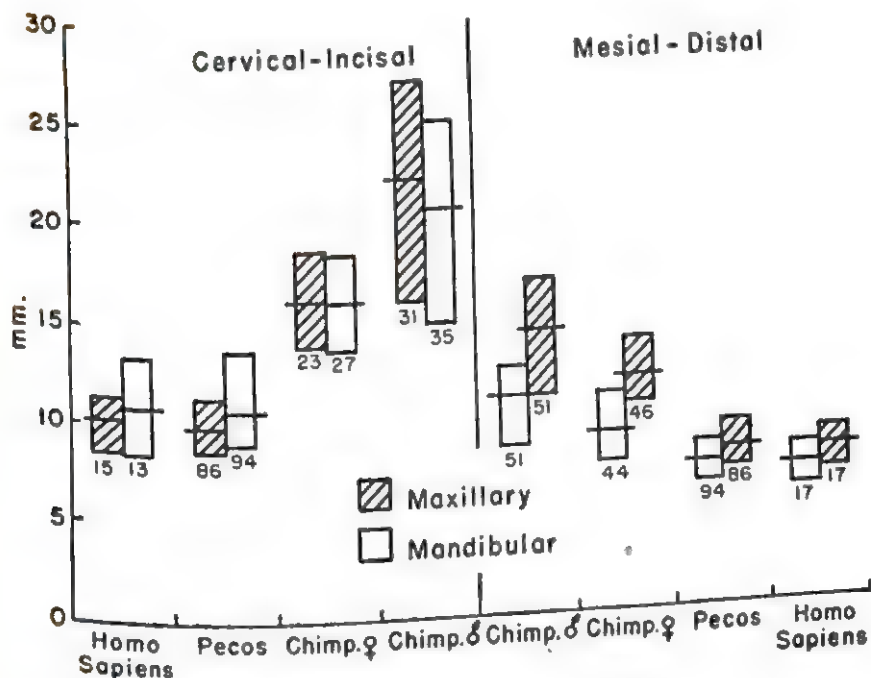


FIG. 6. MEAN VALUES AND RANGES OF CHIMPANZEE AND HUMAN CANINES.

Vertical bars indicate extent of ranges.

Cross lines indicate mean values.

Numerals at bottom of each bar indicate size of sample.

of chimpanzee central incisors are well beyond those of human central incisors. Again, the mean diameters and ranges of the chimpanzee lateral incisors exceed those of human groups with one exception: the ranges of maxillary lateral incisors of chimpanzee, Australian, and *Homo sapiens* overlap.



## PART II

## MORPHOLOGIC VARIATIONS

*Mandibular Molars*

Because of their evolutionary significance, there has been considerable interest in the various occlusal patterns of mandibular molars. The pattern ancestral to anthropoid and human molars was first observed

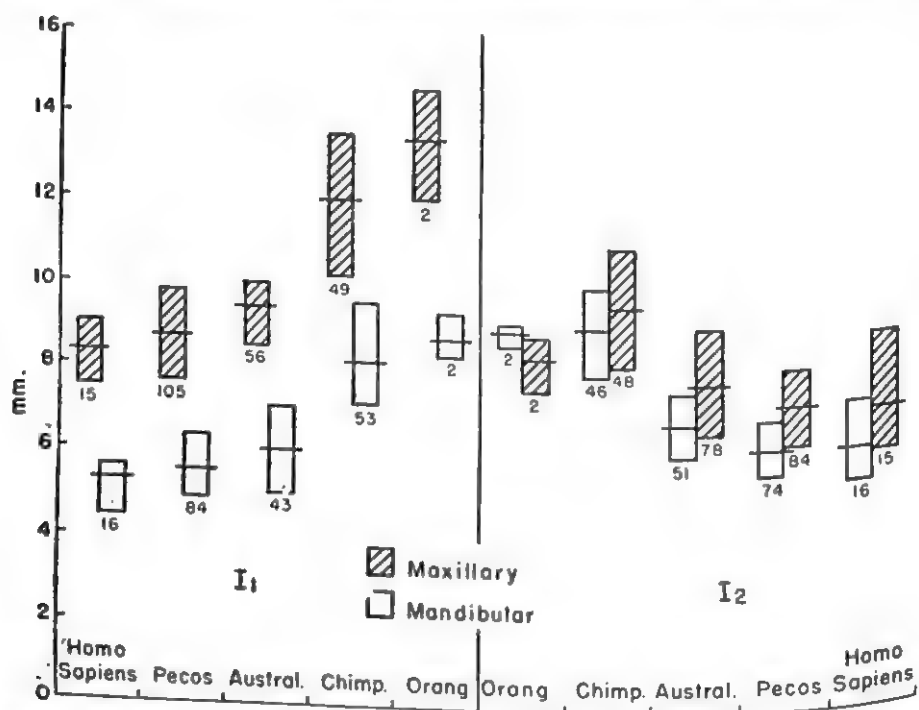


FIG. 7. MEAN VALUES AND RANGES OF MESIAL-DISTAL DIAMETERS OF ANTHROPOID AND HUMAN INCISORS.

Vertical bars indicate extent of ranges.

Cross lines indicate mean values.

Numerals at bottom of each bar indicates size of sample.

in the fossil ape, *Dryopithecus* (Gregory, '22). The Y5 pattern illustrated in figure 4 is considered to be typical of all the *Dryopithecus* molars, and any departure from this configuration supposedly represents a later phase in the evolution of molars. All of these features have been described in detail by Gregory and Hellman ('26, p. 105). For our purpose a brief description will suffice. Cusps 1, 2, 3, 4, 5 are proto-

conid, metaconid, hypoconid, entoconid, hypoconulid, respectively. In the traditional *Dryopithecus* Y $\bar{a}$  pattern, where the three outer or buccal cusps, when viewed from the lingual, form a Y, cusps 3 and 2 are in contact (according to Gregory and Hellman) (figure 8). In the +5 pattern, the 3-2 cusp contact is replaced by the opposite contact, cusps 1-4. Gregory and Hellman have stated that "various intergradations

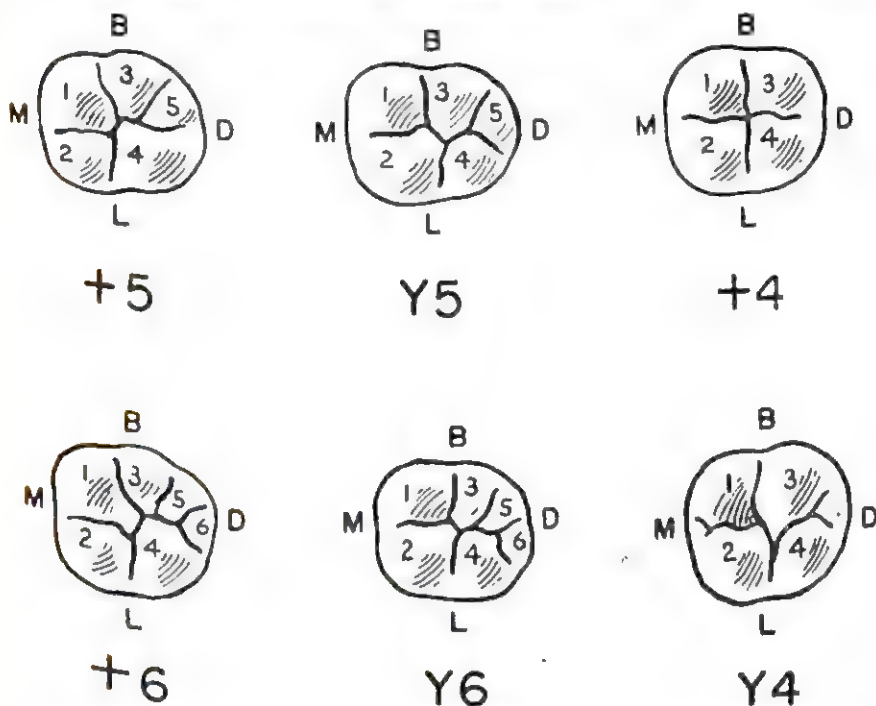


FIG. 8. MANDIBULAR MOLAR PATTERNS IN THE LIBERIAN CHIMPANZEE AND HUMAN DENTITION.

M—mesial, D—distal, B—buccal, L—lingual  
1—protoconid, 2—metaconid, 3—hypoconid, 4—entoconid, 5—hypoconulid

The chief distinguishing feature between "Y" and "+" patterns is the relationship of cusps "3" and "2" to each other. In the "Y" pattern these are in contact, in the "+" pattern they are separated by cusps "1" and "4."

between the primitive *Dryopithecus* pattern with the complete Y and the typical plus-shaped human pattern have been observed . . ." We are in hearty agreement with this statement as a result of our efforts to analyze and categorize the various patterns. Too frequently a Y configuration is seen without the conventional cusp relationship that is supposed to accompany it.

In Y4 (figure 8) cusps 2 and 3 are in contact with 1 and 4 separated.

The various 6-cusp patterns in figure 8 follow the basic 5-cusp configuration with merely the sixth cusp added to the distal portion of the occlusal surface.

The distribution of mandibular molar occlusal patterns of the Liberian chimpanzee is seen in table 7. Since no appreciable sex differences

TABLE 7

*Distribution of Mandibular Molar Patterns in Liberian Chimpanzee*

Total No. of Teeth		Percentage Distribution					
		Y5	+5	Y4	+4	Y6	+6
M <sub>1</sub>	96	54	16	0	2	25	4
M <sub>2</sub>	99	16	59	..	1	9	16
M <sub>3</sub>	114	1	71	..	24	..	5

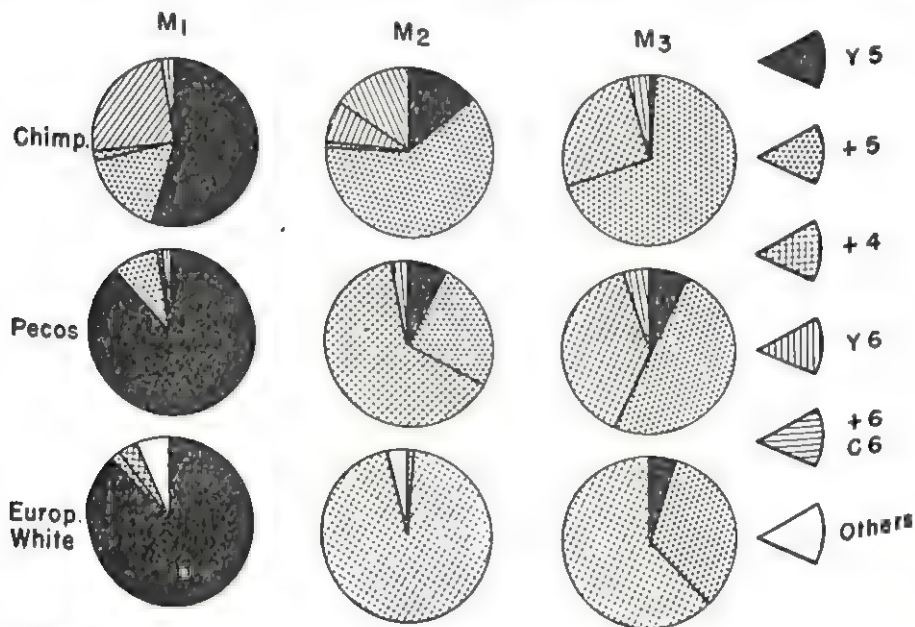


FIG. 9. MANDIBULAR MOLAR PATTERNS IN CHIMPANZEE, PECOS INDIANS AND EUROPEAN WHITES.

were observed, the male and female distributions were consolidated. The Y4 pattern does not seem to occur in the Liberian chimpanzee, and this parallels its low incidence in human molars.

The distribution of molar occlusal patterns in the Liberian chimpanzee is compared to those in human groups (figure 9). The

comparatively low incidence of the Y5 pattern in the chimpanzee first molar is contrary to the expectation that the primitive or ancestral pattern should occur at least as frequently as it does in man. However, 25% of chimpanzee  $M_1$ 's show the Y6 pattern giving a combined (with 54% Y5) total of 79% Y configurations in  $M_1$  and is therefore comparable to the Y incidence in human first molars. Other investigators either did not record 6-cusp teeth, or when they did, neglected to designate the pattern of these teeth.

Compared to the mandibular second molar of human dentition, the Liberian chimpanzee shows a persistence in the retention of a higher incidence of Y patterns (Y5 and Y6 combined). On the other hand, Pecos Indian and European White second molars present a high frequency of 4 cusps, while this trend in the chimpanzee is practically non-existent. The third molar of the chimpanzee tends to be 5-cusped more frequently than do human third molars, although 24% of chimpanzee  $M_3$ 's have only 4 cusps. In general, as to occlusal pattern and the number of cusps, the mandibular molars of the Liberian chimpanzee retain the primitive or ancestral traits to a greater degree than do corresponding molars in Pecos Indians and European Whites. It is of interest that while Y patterns are practically non-existent in the chimpanzee  $M_3$ , the two human groups show appreciable percentages of this pattern in their  $M_3$ 's.

### *Maxillary Molars*

The reduction in size of the hypocone (disto-lingual cusp) of maxillary molars is considered to be another hallmark of the later phases of dentition evolution. In human molars, the hypocone is progressively reduced from  $M_1$  to  $M_3$  and very frequently is completely absent in  $M_3$ . The fate of the hypocone in chimpanzee molars is recorded in table 8. Five size grades are listed. In  $M_1$  is found the highest percentage of large cusps;  $M_2$  is dominated by medium cusps and  $M_3$  by submedium cusps. Also  $M_1$  contains the greatest percentage of smallest (slight) cusps. Three cusp maxillary molars were not observed. In several cases, the internal (mesio-lingual) cingulum extends distally onto the occlusal surface, making it difficult to distinguish such extensions from the presence or absence of a hypocone.

In figure 10 it is seen that the reduction in the size of the chimpanzee hypocone is of a trend similar to that of human molars; that is, reduction from  $M_1$  to  $M_3$ .

TABLE 8

*Reduction in Size of Hypocone from  $M_1$  to  $M_3$  in Liberian Chimpanzee*

	Size	$M_1$ %	$M_2$ %	$M_3$ %
1	(slight)	0	1	19
2	(submedium)	1	10	52
3	(medium)	19	55	27
4	(large)	61	31	3
5	(very large)	19	3	0
	No. Teeth Observed	182	197	186

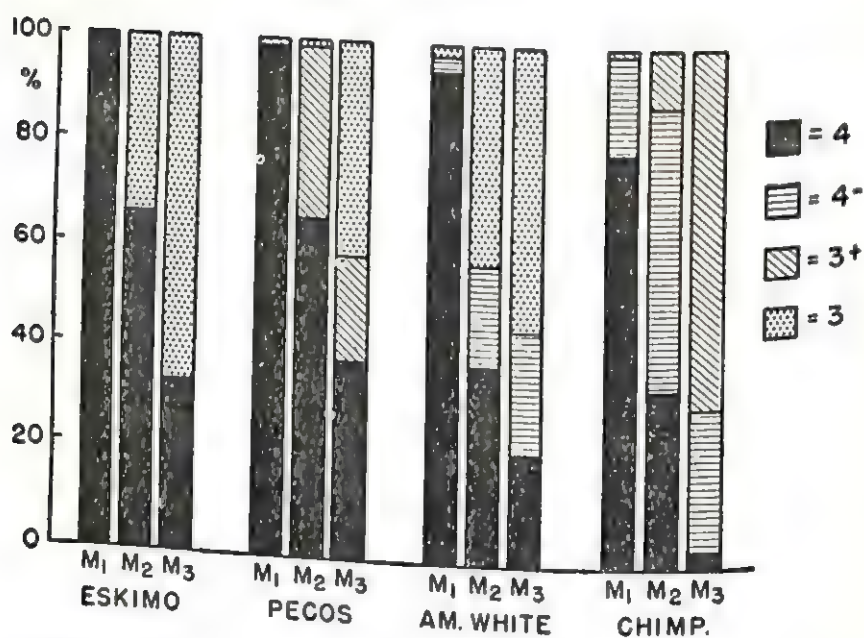


FIG. 10. REDUCTION IN SIZE OF HYPOCONE IN LIBERIAN CHIMPANZEE COMPARED WITH HUMAN GROUPS.

Size grades 5 and 4 (table 8) are combined to represent "4" in this illustration. Likewise, 3 (table 8) equals "4-"; 1 and 2 (table 8) equal "3+."



An anatomical feature observed in high frequency on the maxillary molars of the chimpanzee is the lingual cingulum. On  $M_1$  this is usually confined to the lingual aspect of the protocone (mesio-lingual cusp). On  $M_2$  this same cingulum is usually larger in all aspects and is extended more distally than it is in  $M_1$ . In  $M_3$ , the cingulum, while not of the absolute size found in  $M_2$ , is often relatively large compared



FIG. 11. THE MAXILLARY MOLAR CINGULUM OF CHIMPANZEE COMPARED WITH THE CARABELLI CUSP OF HUMAN DENTITIONS.

- A. *Chimpanzee*. This illustrates the marked increase in size of the  $M_2$  cingulum compared with  $M_1$ . In  $M_3$  it appears that the cingulum is relatively large. Also, the cingulum here coalesces with the hypocone (disto-lingual cusp).
- B. *American White*. The Carabelli cusp is much larger in  $M_1$  than in  $M_2$ .

with the whole crown. Also in  $M_3$ , the cingulum may be extended even more distally than is the case in  $M_2$ , frequently to a point where it reaches the occlusal surface and seems to coalesce with the hypocone. The  $M_1$  to  $M_3$  progression of the cingulum is viewed in figure 11A. In human molars, a cusplet or cusp, known as the Carabelli tubercle, appears in the same location as does the cingulum of chimpanzee molars.

that is, on the lingual aspect of the mesio-lingual cusp. However, unlike the chimpanzee cingulum, the Carabelli structure is largest in  $M_1$ , occurs infrequently in  $M_2$ , and rarely in  $M_3$  (figure 11B). Also it progressively decreases in size from  $M_1$  to  $M_3$  if present in two or more teeth. The foregoing descriptions suggest that the cingulum of the chimpanzee is unrelated to the Carabelli cusp. However, Bolk ('15) and other investigators have observed that there is a more distal location of the Carabelli cusp when it occurs on  $M_2$ , thus agreeing with the distal extension of the chimpanzee  $M_2$  cingulum; Bolk also describes the "band-like" appearance of the Carabelli cusp on  $M_1$  (possibly resembling a cingulum?). Gregory ('22, p. 154) concludes that "the presence of the external cingulum at the antero-internal corner of the first and second upper molars in primitive anthropoids . . . provides us with a starting point for the human line of specialization. . . ."

Appropriate to the cingulum-Carabelli controversy, to the scope of this paper in particular, and to our anthropological times in general, are a few lines from Gregory written in 1922 (p. 358):

Whether or not the Piltdown jaw belongs with the skull, the fact remains that its contained lower molars are in many respects extremely like those of chimpanzees. But these, in turn, are closely related in pattern to human molars; and the whole Piltdown controversy serves to emphasize not only the fundamental agreements, but even the numerous special resemblances in structure of the jaws and teeth of chimpanzee and man. ,

In fully supporting this comment by Gregory, we are of the opinion that even the most astute odontologist could neither infallibly nor with a very high degree of consistency, distinguish between the molars of chimpanzee and man. The probability of such a distinction is further diminished when even a moderate degree of tooth wear has taken place. Observations by one of us (Schuman, unpublished data) reveals the fact that all of the varieties of patterns of tooth wear that occur in man also occur in chimpanzee and these range from flat to markedly oblique wear. These tooth wear patterns imply lateral movements of the mandible, and minimize the limiting factors usually attributed to anthropoid canines in this function. In addition to the metric and morphological similarities of the dentitions of man and chimpanzee, identical histological structures have been observed by Schuman and Sognnaes ('52).

All the observed variations in the dentition of the Liberian chimpanzee are the more significant because of the homogeneity of the group, living in isolation, and sharing a common environment.

## DISCUSSION

With the exception of Pedersen ('49) and Nelson ('38), most investigators have provided insufficient data for comparisons with the metric variations occurring in the dentition of the Liberian chimpanzees. Therefore, in several instances, comparisons of variations are limited to the ranges of measurements. Schultz ('50) utilized ranges of indices to compare the limbs of man with those of other primates. A range composed of the mean, plus and minus two standard deviations, is probably a more valid method for comparing two or more series than is the comparison of their total ranges. Unfortunately, this device cannot be widely applied in the present study since standard deviations are available only in the Pecos Indian and East Greenland Eskimo groups. Where total ranges of measurements overlap only slightly, the use of the "limited" range (mean plus and minus two standard deviations) may serve to separate the ranges. A case in point is that of the mandibular canines of the Pecos Indian and female chimpanzee, where there is a slight overlap in the total ranges of mesial-distal diameters, 8.8-13.6 mm<sup>2</sup> and 13.5-18.3 mm respectively. This overlap is eliminated when the range of mean plus and minus two standard deviations is applied; the ranges are altered to 8.8-12.4 mm and 13.4-18.2 mm. However, in the East Greenland Eskimo, Pecos Indian, and Liberian chimpanzee, the total ranges of molar and premolar diameters overlap so extensively that the application of the limited ranges does not eliminate the overlapping.

The various illustrations of overlapping ranges of diameters in the dentitions from different species makes it apparent that the classification of a single tooth specimen on the basis of mean values and/or modules is a dubious procedure; it remains so even when sufficient data exist to produce statistically significant differences between the mean diameters of teeth from various groups. Another problem of classification is seen in the mandibular molars of the chimpanzee, which are of human order in their raw dimensions but which fall into anthropoid category when the trigonid-talonid indices are assayed (figure 5).

The breadth-length indices utilized by most investigators prove to be of little value, since the ranges of all groups (human and anthropoid) overlap, and differences in mean indices do not reflect the relative changes in breadth and length. These relative changes in breadth and

<sup>2</sup> Nelson ('38, p. 265).

length are disclosed in the procedure recorded in table 3, a procedure suggested as a replacement for length-breadth indices.

The continued use of the module as an index of "mass size" should be discouraged, since it not only does not represent mass size, but also tends to obscure the separate relative values of length and breadth diameters of teeth within and between groups.

#### SUMMARY

The metric and morphologic variations within the dentition of the Liberian chimpanzee have been demonstrated along with comparisons of these variations with those occurring in the dentitions of other groups, as follows:

1. *Ranges*: The ranges of chimpanzee molars and premolars overlap those of orangutan and human groups. The chimpanzee male and female canine ranges overlap; human and female chimpanzee mandibular canines tend to overlap in the mesial-distal diameter only. Incisors (except maxillary lateral incisors) of the chimpanzee are distinct in their ranges as contrasted to human incisors.

2. *Coefficients of Variation*: The coefficients of variation in Liberian chimpanzee dentition are similar in order to the coefficients of variation in Pecos Indian and East Greenland Eskimo dentitions. The maxillary teeth in all three groups seem to be more variable than their respective mandibular teeth.

3. *Butler's Field Concept*: Variation in the dentition of the Liberian chimpanzee support the concept as follows:

- a. Coefficients of variation increase with movement away from the polar tooth in each tooth group.
- b. Mandibular molar patterns in the Liberian chimpanzee tend to retain "ancestral Y" configurations in  $M_1$  with a progressive decrease of these configurations in  $M_2$  and  $M_3$ . Also, there is a tendency toward decrease in the number of cusps from  $M_1$  to  $M_3$ .
- c. The decrease in the size of the hypocone from  $M_1$  to  $M_3$  parallels the decrease occurring in human molars.
- d. The cingulum (on the lingual aspect of the mesio-lingual cusp) increases either absolutely or relatively in size from  $M_1$  to  $M_3$ . This may parallel (in reverse) the decrease in the incidence and/or size of the Carabelli cusp in human molars.

4. *Dimensional Variations in the Sequence of the Molar Teeth*:

Neither the human formula  $M_1 > M_2 > M_3$  nor the anthropoid formula  $M_1 < M_2 < M_3$  predominates in a majority of the molar series. Variations of both formulae appear in significantly high percentages.

The metric and morphologic features of the posterior dentition of the chimpanzee affiliate far more closely with man than with gorilla and orangutan.

The molars of contemporary chimpanzee exhibit ancestral patterns (dryopithecus Y configurations) to a degree similar to that occurred in contemporary man. This suggests a comparable evolutionary pattern for the posterior dentition of man and chimpanzee.

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#### LITERATURE CITED


- ASHTON, E. H., AND S. ZUCKERMAN 1950 Some quantitative dental characteristics of the chimpanzee, gorilla and orang-outang. *Philosophical Transactions of the Royal Society of London. Series B*, No. 616, Vol. 234: 471-484.
- BLACK, G. V. 1902 *Descriptive Anatomy of the Teeth*. Fifth Edition. S. S. White Dental Mfg. Co., Philadelphia.
- BOLK, L. 1915 *Des Carabellische Hoekerchen*. *Schweiz. Vierteljahrsschr. f. Zahnheilk.*, 25: H. 2.
- BUTLER, P. M. 1939 Studies of mammalian dentition. Differentiation of post-canine teeth. *Proc. Zool. Soc. London*, 109: 1-36.
- CAMPBELL, T. D. 1925 Dentition and palate of the Australian aboriginal. Univ. of Adelaide. Ph. D. Thesis.
- DAHLBERG, A. A. 1945 The changing dentition of man. *J. Amer. Dent. Assoc.*, 32: 676-690.
- 1949 The dentition of the American Indian. *Papers on the Physical Anthropology of the American Indian*. The Viking Fund, New York. Pp. 138-176.
- GREGORY, W. K. 1922 *The Origin and Evolution of the Human Dentition*. Williams and Wilkins Co., Baltimore.
- GREGORY, W. K. AND M. HELLMAN 1926 The Dentition of Dryopithecus and the origin of man. *Anthrop. Papers of the Amer. Mus. of Nat. Hist.*, Vol. 28, Part I.



- HRDLÍČKA, A. 1923 Dimensions of the first and second lower molars with their bearing on the Piltdown jaw and man's phylogeny. *Amer. J. Phys. Anthropol.*, 6: 195-216.
- NELSON, C. T. 1938 The teeth of the Indians of the Pecos Pueblo. *Amer. J. Phys. Anthropol.*, 23: 261-293.
- PEDERSEN, P. O. 1949 The East Greenland Eskimo dentition. *Meddelelser om Grønland*, 142. København.
- SCHREIDER, E. 1953 Quelques problèmes préalables à toute recherche de biometric physiologique: Variations intraindividuelles, etc. *Biologie*, 12: Nos. 1, 2, 3, 4.
- SCHUMAN, E. L., AND R. F. SOGNAES 1952 Surface texture and histologic structure of chimpanzee teeth; procedures and preliminary observations. *Amer. J. Phys. Anthropol.*, n.s. 11: 246.
- SCHULTZ, A. 1950 The physical distinctions of man. *Proc. Amer. Phil. Soc.*, 94: No. 5.
- SENYUREK, M. S. 1939 Evolution of human dentition. A metrical approach. Part II. Ph.D. Thesis, Peabody Museum of Amer. Arch. and Ethnol. Harvard University.
- SHAW, J. C. MIDDLETON 1931 The teeth, the bony palate and the mandible in Bantu races of South Africa. John Bale Sons and Danielsson, London.
- SNEDECOR, G. W. 1950 Statistical Methods. Iowa State College Press, Ames, Iowa.
- STEIN, M. R., AND J. L. EPSTEIN 1934 The molar teeth of New Britain Melanesians. *J. Amer. Dent. Assoc.*, 21: 1409-1413.



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# TENTATIVE GENERALIZATIONS ON THE GROUPING BEHAVIOR OF NON-HUMAN PRIMATES \*

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## INTRODUCTION

THE purpose of this paper is to formulate tentative generalizations about grouping behavior of non-human primates. The need is great for attempts to construct a conceptual system to give direction, form and significance both to collected data and to on-going research.

This paper is a condensed revision of a contribution to an international symposium held in Paris in 1950. The symposium was reported in a monograph entitled *The Structure and Physiology of Animal Societies*.

It may be premature to attempt to formulate generalizations and sketch the parameters of grouping behavior of primates. Available information is sketchy. The requirements of adequate sampling have not been applied to the selection and study of different types of orders, families, genera and species. Field investigations and experimentations have been integrated only to a very limited extent. Qualitative studies have not been balanced with quantitative studies on social interactions.

The generalizations which will be stated should be considered as hypotheses needing further proof or disproof. It is never premature in science to formulate hypotheses provided they are understood as such and not accepted as established principles.

\* This paper is a summary of a more extensive study. See Carpenter '52.

## BASIC ASSUMPTIONS

It may be useful to review several assumptions basic to comparative studies of social behavior. Although these assumptions are taken for granted by those of us who do research in the field, some are rejected, either explicitly or implicitly, by many of our colleagues. These assumptions are the following:

- A. That the general principles of scientific methodology are eminently appropriate for investigating behavioral interactions of organisms, including grouping behavior, social stimuli and responses, social organization, and even complex cultural processes.
- B. That a central task of comparative research on social behavior is to describe and measure, if possible, the central tendencies or commonalities of such behavior as well as its variabilities or differences.
- C. That all levels of complexity of interactional social behavior operate within a tissue of ordered, interactional forces and deterministic energy systems.
- D. That in the phylogenetic scale organisms and their behavior tend to become more complex from the so-called "lower" to "higher" forms, and that increasing complexity may result in differentiated "emergents."
- E. That the analytic approach dealing with problems in an order varying from the simple to the complex is a justifiable scientific approach.
- F. That a principal justification for investigating and striving to understand the social adaptations and adjustments of non-human primates is to add to the information and advance our understanding of the social adaptations and adjustments of man.

The following are assumptions which for us are untenable. Nevertheless, they are accepted, either implicitly or explicitly, by many of our colleagues, and in the interest of intellectual integrity we must argue their validity.

- A. That the primate *Homo sapiens* differs so greatly from all other genera of the order Primates, especially on the level of complex social behavior, that investigations and data of non-human primates have no significant relevance to understanding the deter-

minants of human behavior or, conversely, that the similarities of the two are so great that identity can be assumed.

- B. That the phenomena known as "mind," language, society, culture and "values" exist exclusively on the level of human evolution.
- C. That explanatory systems can consist of dichotomous, over-simplified concepts such as heredity-environment, physical-mental, emotional-rational, implicit-overt, natural-supernatural, individual-social and animal-human.
- D. That the predominantly important determinants of social adjustment operate in external situations or, conversely, that genetic determinants in the organism are of predominate importance in determining social behavior.

These and similar untenable assumptions have led to prevalent *homocentric delusions* which pictures man abstracted out of his biotic context, as dissociated from his supportative base of natural resources and as living and merely acting in response to the currents of "social" forces. Furthermore, the conflict of basic assumptions which we have outlined above has led to disassociations of the biological and social sciences and to the "foreign" languages of different academic disciplines. One example is the fantastic verbiage which has been developed by psychoanalysts and psychiatrists to describe sex behavior, aggression, and reaction to social controls of the individual.

Let us now attempt to formulate tentative generalizations for some of the major features of grouping behavior.

#### SPATIAL DISTRIBUTION

A basic approach to the study of grouping behavior in non-human primates is that of describing the objective, observable and perhaps measurable spatial distributions of populations and organized groups. Non-human primates are restricted in their geographic distribution and adaptations to climates and biotic environments of tropical and sub-tropical regions. Why? Apparently because they do not migrate, hibernate, store food nor build shelters which effectively protect them from weather. Thus, we may generalize (1) that non-human primates lack adaptive and adjustive capabilities for coping with those degrees of climatic variations and fluctuations in food supply other than those variations typical of tropical and semi-tropical regions.

Within geographic ranges and in population segments, organized groups of types which have been studied show strong tendencies to adjust to limited territories. These territories are occupied, possessed and defended against other organized groups of the same species. However, groups of other species or genera are tolerated within territories. The evidence seems to be adequate to support the generalization (2) *that organized groups of non-human primates adjust to limited territorial ranges and defend these territories against other organized groups of the same species.*

Within territories, organized groups arrange themselves in patterns of group scatter. Different genera exhibit different but characteristic grouping patterns. The average spatial arrangements of individuals to each other in a group, ignoring variations introduced by disturbed actions, would seem to express, or be indicators, of strengths of attachment, interdependence or probabilities of interactions among members. From this we may derive a third generalization (3) *that individuals in free-ranging organized groups deploy themselves in space in an inverse relation to the strength of positive interactional motivation and conditioning and in direct relation to the degree of negative motivation and conditioning.* This generalization could be transformed into an expression of interaction probabilities. Exceptions occur for fighting in which antagonism of some degrees results in close-in hostile behavior.

#### COMPOSITION OF GROUPS

Sufficient information is available to permit formulating several important generalizations about the composition of non-human primate groups. The first of this series is: (4) *that the sizes of groups in undisturbed populations varies within definable limits and around central grouping tendency characteristic of a genus.* This generalization indicates that the sizes of groups fluctuate within each species or genera and that there are size differences for different genera. The comparative research problem becomes that of determining what factors influence the number of animals in groups and what factors operate in various species or genera to produce inter-genera variabilities. Age of the organized group, reproductive rate, group division and population density are known to affect group sizes. The number of animals and their characteristics importantly affect the behavior of individuals and the group as a whole.



## CENTRAL GROUPING TENDENCIES

Records of central grouping tendencies for different types provide additional descriptive information which can be compared for different types. The following are expressions of median groupings for three representative types:

## Howlers

3 adult males + 7 adult females + 2 infants + 4 juveniles  
+ unknown number of males living alone

## Spider Monkeys

2 adult males + 4 adult females + 2 infants + 4 juveniles  
+ extra group males living in groups

## Gibbons

1 adult male + 1 adult female + 1 infant + 3 juveniles  
both males and females living alone temporarily.

Confidence is high in the reliability of the expressions for howlers and gibbons but low for spider monkeys. Recently, recalculations on population data of howlers of Barro Colorado Island for 1935 and that published by Collias and Southwick ('52) show that percentages of different categories to total population in groups remain relatively stable even after marked reduction in the total population and the consequent reduction in the size of groups. These data lead to the fifth generalization: (5) *that proportions of different classes of animals in groups with respect to age and sex is more stable than the total size of groups.*

## SOCIONOMIC SEX RATIO

In the non-human primate groups which have been studied, extra-group individuals have been observed. In most genera, these extra-group animals are males, but in gibbon populations both "solitary" males and females are observed. These animals apparently reflect differences in the ratios of adult males and adult females living within groups since in most there are fewer males than females. Thus, we come to a generalization on this intra-group socionomic ratio which seems to be a function of basic social adjustments. The relevant generalization is: (6) *that the composition and stability of primate groups is strongly affected by the relative balance of male with female sexual hungers and capacities and reciprocal satisfaction among adult members of groups.*

## STATUSES OF INDIVIDUALS IN GROUPS

Status is an ordinal concept applicable to individuals arranged on the basis of behavioral data along a gradient scale or continuum. Individuals have status only relative to other individuals. The definition of social gradients of behavior and interactions within groups is one approach to describing the structure of groups. There are probably many such definable gradients, e. g., rights of access or possession, prestige or behavioral effects, spatial positioning "privilege" and dominance-subordination. Of these the latter has been investigated most and is best known. The relevant generalization is: (7) *that in non-human primate groups there exist ordinal series of positions or definable continua or gradients which represent for individual animals, relative to others, the probabilities of occurrence of definable kinds of overt behavior.* And, for our purpose, the variously defined behavior of "dominance" may be sketched by the generalization (8) *that the probability of access to incentives appropriate to activated drives of interacting animals defines the dominance statuses of individuals.* Several subordinate facts are noteworthy: Dominance for a given individual, in a given group context, tends to be relatively constant; nevertheless variations occur in the drive strengths of interacting individuals. Also, a kind of *social summation* of statuses may occur when individuals are closely associated. Also, an individual may *derive* status from association with another or other individuals. In extreme cases, finally, and with few individuals, supreme, exclusive and generalized statuses may be attained. All statuses in primate groups must be continuously maintained. Status may be lost gradually or suddenly.

## GROUP CONTROL

Organized groups have behavioral systems for regulating and controlling their actions. In the past these have been inadequately described by emphasizing for most types the anthropomorphic concept of "leaders." Therefore, another generalization is in order: (9) *that the control of a group is distributed among individuals and classes of individuals in direct proportion to the statuses of individuals or classes of individuals.* Control potentials are learned by group members and control is often exercised through signal or cue behavior associated with specific individuals and their actions.

## INTEGRATION

Groups of non-human primates exhibit observable behavior which indicates varying degrees of group integration. Some of these indicators are the number and kinds of individuals which join or leave the groups, the variations in group scatter or spatial patterning, the amounts of intra-group conflict, degrees of concerted action, etc. Conceivably, the integration of groups is affected by both centripetal and centrifugal types of behavioral interactions. What then determines the direction and degrees of these "social movements"? This brings us to the tenth generalization: (10) *that the vector sums of the centripetal and centrifugal forces equal the degree of group cohesion or integration, and in turn, the drives, tensions or needs of individuals interacting with incentive behavior of other individuals both modify and stabilize the total network of interactions in the group.* Simply stated, many of the drives of each individual are satisfied, or reduced by interactions with other individuals. The interactions are reciprocal and this reciprocity of interaction principle is considered to be very fundamental in the dynamics of groupings. The principle refers to organism-behavior characteristics which can never be neglected in the study of social behavior however difficult the task of specifying and measuring the dimensions of these interactions.

At this point let us revert from considerations of groups as wholes to the basic elemental unit. In the study of complex groups it will often be necessary to limit observations or measurements and to provide for controls. This brings us to a methodological generalization: (11) *that the basic interactional unit is the reciprocal stimulus response interactions of one individual with another symbolized by  $O^1 \rightleftharpoons O^2$ .* A definition of this generalized unit of study involves describing  $O^1$  and  $O^2$ , defining the quality of behavior, describing or measuring interactional factors and effects and describing the context in which the animals act. *It is believed that this unit can be systematically extended to cover the total number of paired interactional possibilities of a group which equals  $\frac{N(N-1)}{2}$ .* Experimentation under controlled conditions using the  $O^1 \rightleftharpoons O^2$  unit has been fruitful and remains promising.

## AUTONOMY OF GROUPS

Organized groups of non-human primates tend to be autonomous; they are capable of maintaining, regulating and controlling themselves largely independently of aid or assistance from other groups. However, they are only semi-closed, since there are exchanges of members from group to group, under some conditions, thus providing for "out-breeding." The relevant generalization is: (12) *that organized groups of non-human primates tend strongly to be autonomous, self-maintaining and regulating.* Such groups express resistance and hostility to other organized groups of the same but not different species (genera).

These propositions set the stage for a final generalization: (13) *that organized groups of a population of the same species in a limited region do not have supergroup social mechanisms.* Groups are not included in tribes, clans, communities, etc. as are found on the human level. Kinship relations are not operative and inbreeding is the rule rather than the exception to the normative behavior of non-human primates.

## LITERATURE CITED

- CARPENTER, C. R. 1952 Social Behavior of Non-human Primates. Structure et physiologie des sociétés animales, Colloques Internationaux du Centre National de la Recherche Scientifique, 34: 227-246, Paris, Mars 1950.
- COLLIAS, NICHOLAS, AND CHARLES SOUTHWICK 1952 A field study of population density and social organization in howling monkeys. Proc. Amer. Philosophical Soc., 96: 143-156.





## PROBLEMS OF MENTAL EVOLUTION IN THE PRIMATES

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THE inclusion in this symposium of four papers dealing with behavior is a measure of the increasing importance assigned to behavioral phenomena in their relevance for the general problem of evolution. This relevance, recognized since even before Darwin, still needs to be underscored. The fact that the theory of evolution as we know it today is founded primarily on structural evidence is understandable enough, since structures leave a record whereas physiological processes and behavior for the most part do not. It might well be that if we had a record of behavior as complete as the fossil record of structures, this would yield as convincing a body of evidence for evolution as does the latter. As a matter of fact, a study of the behaviors of living species alone—together with the paleontological evidence regarding the order in which these forms appeared—provides in itself a substantial basis for postulating a process of evolution. It is true, also, that here and there behavioral criteria have been found useful in supplementing structural evidence in problems of taxonomic classification (e. g. Lorenz, '37).

In the hierarchy of life sciences, psychology or the study of behavior occupies a rather unique position. On the one hand, it represents the most complex unit, the highest level of organization, dealt with by any of the so-called biological sciences. On the other hand, it represents the unit from which all the social sciences take their start. Among the sciences, therefore, psychology is a sort of two-way funnel into which the biological sciences converge and from which the social sciences diverge.



It happens, also, that scientists—all scientists—are individuals and primates. This makes it not only natural but inevitable that we should be egocentric and anthropocentric in our interests. The essence of the individual is his behavior, including his feelings, attitudes and strivings. His bones, muscles, and blood chemistry are in this respect secondary, being the conditions necessary for behavior. Psychology thus represents the most direct approach to what is of most immediate interest to man. And comparative psychology is concerned with the phylogenetic or historical basis of man's behavior.

More to the point in the present connection is this: that if we think of evolution as having a direction—this direction being a *post hoc* inference from observation and thus implying no guiding purpose—then this direction is most readily defined in terms of a trend in behavior. As we shall see, behavioral differences are especially striking within the order of primates. We of course assume that a trend in structural change—specifically change in the nervous system—underlies the behavioral trend, but as of now the former is even less clearly defined than is the latter. This statement is not necessarily inconsistent with one of the main points I wish to make today: that one of the weakest links in the sciences dealing with evolution, the one most needing to strengthen its facts and theoretical framework, is that dealing with behavior. I should also introduce here a word of explanation about what follows in this discussion. Of the 50-odd living genera of primates (Simpson, '45) only a very few have been studied to any extent in regard to behavior: man, chimpanzee, the macaques and cebus monkeys. Our discussion of behavior, therefore, cannot give anything like the extensive comparisons within the order as did some of the previous papers. We shall have to content ourselves with the grosser distinctions between the few aforementioned primates.

In a survey of behavior from ameba to man we find both similarities and differences, depending largely on the scale of observation used. In general, the similarities are expressed in terms of function or adaptive outcome. The differences are quantitative or refer to details of mechanisms which have more or less the same results. That is to say, the evolutionary development of behavior shows a continuity which parallels that of physical structures. There is, however, one possible exception. Whereas the physical differences between man and some of the other primates are no greater than those found at many points along the phylogenetic scale, the behavioral differences between *Homo sapiens* and

the living nonhuman primates exceed those found anywhere else. They are so striking that the possibility of a break in the continuum, of a qualitatively new emergent, may be and is widely entertained. Simpson ('49, p. 286) for instance, characterizes man as "fundamentally a new sort of animal" with a "new sort of evolution." The "new sort of evolution" refers, of course, to culture, or, as he puts it, "the inheritance of learning." The importance of culture as an offshoot of organic evolution, and with almost limitless possibilities of development, has been stressed by many writers. Few would deny that it is an almost uniquely human achievement. It is a social phenomenon in that we are all affected by culture and in varying degrees contribute to it. Nevertheless it is, in the last analysis, a product of the human individual; it has to be "invented" as well as used. It is in the characteristics of the individual, therefore, that we must seek its explanation. Simpson ('49, pp. 291-92) goes on to say that the human species "has properties unique to itself among all forms of life." These properties of the individual include especially "the accumulation of knowledge, . . . a sense of values, and the possibility of conscious choice." ('49, p. 290). As I shall try to show later, the differences in knowledge and in "a sense of values" are basically quantitative.

Let us consider first the chronically vexacious problem of consciousness. Is man the only conscious animal, or is he merely more conscious than others? Or could it be that some animals are more conscious than man? These are obviously hopeless questions. The only consciousness that we can observe directly is our own, personal awareness. And especially since Freud, we know that conscious content gives only a partial and highly prejudiced account of the factors actually determining behavior. In comparative psychology, certainly, we cannot use conscious processes as data. This fact has no implication for the question of whether animals are, or are not, conscious. Our best guess may be that consciousness is a quantitative rather than all-or-none phenomenon and that it appears in some degree in animals other than man. Having worked with chimpanzees for a number of years, I have no doubt that these animals are sometimes angry, resentful, jealous, remorseful, affectionate, happy or sad; that they have intentions and expectations which may be frustrated or satisfied. This conviction probably influences the design of my experiments but is almost worthless in reporting my results. Mentalistic terms are a convenient, short-hand way of designating and classifying various sorts of behavior, but they do not furnish any useable

data. The term "mental evolution" in the title of this paper was intended to convey the idea that most or all of those forms of behavior, which in us are accompanied by awareness, can be seen also in the higher nonhuman primates. Whether in them those behaviors are accompanied by awareness is irrelevant; the behaviors themselves, and their mechanisms, are legitimate material for comparative psychology and are pertinent to the general problem of evolution.

The phenomena to be considered in a phyletic comparison of behavior may be grouped into three classes: 1) the realm of cognitive or intellectual functions—all those problem-solving capacities which we often lump under the term "intelligence"; 2) the emotional and motivational aspects of behavior; and 3) these first two classes in their social-cultural manifestations. In each of these fields evolutionary progression (or succession) has been characterized in various ill-defined ways. It is said that as we "go up" in the phyletic scale we find a greater range, diversity, and complexity of intelligent behavior; more flexibility or plasticity versus rigidity; increased learning capacity. Some intellectual functions, such as abstraction and symbolism, are usually ascribed only to the "highest" animals. The needs of the organism increase in number and complexity. Play, exploration and curiosity become more prominent as motivators of behavior. The forward reference of striving and planning encompasses longer periods of time. There is, in general, greater socialization, specialization and division of labor among individuals; and social organization becomes increasingly independent of genetic determination. This list could be greatly extended but is long enough to illustrate how vaguely phylogenetic differences in behavior are usually formulated. The first need, obviously, is the analysis of these gross descriptions into their components. To say that man differs from other primates in his capacity for tool-making and language is not very useful until we have identified the mechanisms or processes which produce these complex end-results.

Our problem is one of measurement: to measure the differences and similarities of behaviors exhibited at various phylogenetic levels. Before we can measure we need, first, axes or continua of variation, and second, units in terms of which differences along the axes may be described. In the physical world we have such axes as length and such units as inches. In psychology we have good measures of certain basic functions but as yet relatively few clearly defined dimensions of variation and units of measurement for the higher levels of behavior. In respect to

the basic or relatively simple functions, the measures indicate very little difference between the primate species which have been tested. Visual acuity, for instance, is almost the same in man and chimpanzee (Spence, '34); color vision is slightly better in man than in chimpanzee and rhesus monkeys (Grether, '39, '40). Simple reaction time—the speed with which an organism can respond to a signal—is the same for young chimpanzees and human children of comparable age (Forster, '35). In the speed of forming those uncomplicated associations known as classical conditioning, there appear to be no differences between the most primitive and the most highly developed animals (Razran, '33). In remembering a well-practiced task or association over long periods of time, the available data show no differences among the primates which have been tested (Nissen, '51a). Phylogenetic differences, and especially those critical for a comparison of the lower and higher primates, are evidently to be sought in what we loosely refer to as the “higher mental functions.” And these functions, as I have indicated, are as yet imperfectly defined. I might say, parenthetically, that the same difficulty confronts the testers of human intelligence. For the most part their measures of mental age and IQ are based on unanalyzed end-products, with little knowledge of the functions which entered into the test-performances.

The difficulties of measurement, and also our earlier rough survey of phylogenetic differences, suggest a phrase which characterizes these changes: increasing complexity. This term is obviously descriptive rather than explanatory and is too broad, to be useful unless the complexity is further specified. I suggest that complexity be defined in terms of the sheer number of factors which determine behavior. The number of determinants may increase both spatially and temporally. In the lowest organisms the most intense stimulus of the moment tends to govern the reaction. Later, the reaction is increasingly determined by a number of concomitant stimuli that influence each other by summation, inhibition, and so on. In vision, for instance, light intensity and direction govern the responses of the protista. In higher invertebrates, light distribution or patterning also becomes effective. The cumulative effects of previous experience become major factors in governing response to present stimulation, and this influence extends to more remote time. This temporal integration, I should point out, is a function of the individual. It is tempting to analogize and to say that the time-binding capacity of man extends to the race, via culture. But this is only an analogy. Education, imitation and so on are special ways of having



experience; the integration of those experiences is still a function of the individual.

A formal experiment may serve to illustrate the proposed dimension of increasing behavior determinants (Nissen, '51b). A chimpanzee is trained that choice of the larger of two square white plaques is rewarded, whereas choice of the smaller one is not rewarded. He then learns that if the two squares are black, the smaller one is correct. After these two habits are learned, he finds out that if the plaques are triangular instead of square, the previous relations are reversed; the smaller of the white triangles and the larger of the black triangles are positive. The problem is further complicated until the chimpanzee has to take into account 5 different factors or cues in order to make the right choice. This problem, which puts some strain on a human subject, was mastered by the chimpanzee. A similar experiment conducted by Noer and Harlow ('46) indicates that rhesus monkeys can respond to at least 4 cues. Rodents and carnivores have great difficulty when the number of essential cues exceeds two.

Since behavioral complexity is roughly correlated with phylogenetic level, we may ask whether, in back of this correlation, there is a more fundamental difference in cognitive mechanisms. The relative importance of genetic versus experiential determination would seem to constitute such a difference. This distinction, often referred to as "instinct versus intelligence," is especially clear if we compare, say, the insects and man. In the former, behavior seems to be largely a function of inherited mechanisms, whereas in the latter it is determined more by individual experience. The distinction is usually interpreted as a difference in the rigidity of stimulus-response connections; in the one case a certain response is innately elicited by a certain stimulus or situation, whereas in the other S-R connections are learned. This may constitute one of the differences but, I believe, only a minor one. More important is that in the "lower" animal the repertoire of perceptions is for the most part genetically fixed, whereas in the "higher" animals that repertoire is built up by or in experience. The instinct-guided animal is ready for its species-characteristic behavior almost as soon as it is born; the primate passes through an extended period of helpless infancy and childhood before it is ready for self-sufficient adult behavior. Evidence is accumulating that in chimpanzee as in man the principal learning going on during this time is the formation of perceptions, that is to say, the building up of a knowledge of the world, making sense out of what at



first is an undifferentiated confusion. I have suggested elsewhere (Nissen, '51a) that so-called play behavior provides the experiences which leads to perceptions and knowledge, and that this is why we see so much more play in the primates than in those animals which come equipped with ready-made perceptions, and more in young than in old animals. Experiments conducted at the Yerkes Laboratories with dark-reared infant chimpanzees indicate that the art of seeing, of perceiving contours and patterns, recognizing a milk bottle and the familiar attendant, is the result of prolonged learning or experience. The distinction between acquiring perceptions as contrasted with forming habits or S-R connections is important. The child has the perception of a door when he knows that it is a means of entrance and exit, a way to let in fresh air or to keep out the cold, and so on. He has a door-habit when he always slams the door shut. Perceptions are knowledge which can be used in forming habits or in acquiring other higher-order perceptions. Having learned to perceive squares, circles, triangles and so on, we may then, if we are one of the higher primates, acquire the perception—or as it is more commonly called, the concept—of form. The learning animals, therefore, can multiply their perceptions enormously, and this increase in the number of behavior determinants correspondingly increases the complexity of behavior. The instinct-guided animals, on the other hand, are stuck with their limited number of innately provided perceptions, which increase little with experience and which thus limit behavior to a lower degree of complexity.

In case there are any extreme environmentalists present today, it may be in order to point out here that man and the other learning animals have not actually escaped genetic determination. The potentialities for perception and conceptualization are inherited just as much as is eye-color, and those potentialities are limited in kind and number. With the right inheritance an individual may, under favorable conditions, acquire a great deal of knowledge, but, by definition, he will not become Superman. We are thus assured that experience will not make a man out of a monkey, although the opposite is alleged to occur sometimes.

In respect to innateness of behavior-determination, it is clear that the higher monkeys and apes stand a great deal closer to man than to most other mammals. The chimpanzee seems to have hardly any more instinctive modes of response than does man. Wild chimpanzees regularly build tree nests to sleep in at night, and these nests have a fairly uniform structure. There is pretty good evidence, however, that this

nest building is not instinctive, as in birds, but is, rather, transmitted by imitation or tuition from one generation to the next; it is, therefore, one of the very few items of behavior seen in these animals which may be classified as cultural. Mating behavior, which is highly instinctive in most mammals, is for the most part a matter of trial-and-error learning in the chimpanzee. One of the few behaviors of this ape which may be designated instinctive is grooming, or as it is often called, flea-picking. This appears in the captive-born chimpanzee when there has been no opportunity for imitation or tuition. The stimulus is a shiny object or small irregularity in any surface. In general, however, the perceptions of chimpanzees appear to be as much a product of experience as are those of man; the ape's potentialities are more limited, but certainly much greater than those of nonprimate mammals.

Limitation in respect to the kind of perceptions which an organism can learn is related to the amount of temporal integration involved. The perception of relations such as larger-smaller, lighter-heavier and so on are immediately given in a single experience. Other relations, such as "the middle one of 3, 5, or 7," "the odd one," or "the one which matches the sample" cannot be perceived in a single experience but come from observing the common element in a number of successive experiences. This is true likewise of concepts like "color" and "form." In the conditional matching problem (Nissen, Blum, and Blum, '49) the animal must choose the color-matching object when sign A is present, but must choose the form-matching object in the presence of sign B. Mastery of this problem clearly involves the percepts or concepts of form and color. Although nonhuman primates do solve this problem, it takes them a long time. A human subject can solve it much faster. This difference may be in part a function of the backlog of experience and education, relevant to the problem, which most nonhuman primates do not have when first confronted by the situation. In much larger part, I believe, the difference is a function of a hypothetical mechanism which increases enormously the capacity for temporal integration.

The facts which compel us to infer such a mechanism are the radical increase (a) in the speed with which associations are formed and re-formed, especially those involving higher level relations or concepts, (b) in the facility with which general principles or laws are used as short-cuts to problem solution, and (c) in the number of factors or items which can be utilized in determining response. This mechanism, therefore, does not introduce a new or higher kind of mental functioning,

but it does increase greatly the efficiency with which certain functions, already present in nonhuman primates, are performed. That greater efficiency permits a pyramiding of percepts and concepts, each level building on top of that of lower complexity. Each level operates in two ways: (1) it makes possible the formation of concepts of still higher complexity, and (2) it facilitates the handling of lower level percepts. Problems which the chimpanzee solves by slow and laborious memorization, the human solves easily and quickly by applying a higher level formula or principle. Mathematics furnishes many good examples of this pyramiding process. The name we give to our inferred mechanism is unimportant; if the term had not been so uncritically misapplied in the past I should be inclined to call it a symbolic process. Certainly it is associated with and, in us finds its major expression in, language. It should be emphasized, however, that "language" is two separable things: (a) a method of communication, and (b) a tool or instrument of thinking. If one of these functions has developmental priority over the other, it would seem reasonable to suppose that the use of symbolic processes as an aid to the individual in thinking and problem solving preceded language as a means of communication in social intercourse. At any rate, according to this schema of cumulative pyramiding increasing complexity of behavior determination is in the first place a function of quantitative increase, but this involves new kinds, i.e., higher level, concepts.

If we analyze the process of logical thought, including the formation of concepts, we find that it reduces to three processes: the recognition of differences, the recognition of similarities or identities, and most important, a proper balance between these two. To take a simple example: in the conditional matching problem already referred to, the subject must respond to the differences among colors or among forms, but must also respond to the similarity of various colors as contrasted to forms. Over-emphasis on either similarity or difference interferes with solution. In respect to this balance or, as we may call it, sagacity,<sup>1</sup> the nonhuman primate tends to err on the side of over-responding to difference. In general, the chimpanzee classifies as a scatter-brained individual, very sensitive to difference or change, and unlike the obsessed individual who responds to the similarities between widely divergent

<sup>1</sup> This meaning of "sagacity" is consistent with, but more restricted and specific than, that found in the writings of William James (1890) and Hollingworth ('28).

phenomena. This ape is therefore the "scientific" rather than the "philosophical" type. The species difference in sagacity is, of course, a quantitative one.

I have taken so much time in discussing the cognitive side of behavior that the perhaps more spectacular differences in motivational-emotional aspects, and their expression in social phenomena, will have to be neglected. I shall have to content myself with a bald statement of the thesis that there are no fundamental or qualitative differences between the emotions and motivations of man and the other primates; that the very large and dramatic differences in the expression of emotions and in the organization of motivational hierarchies are secondary, deriving from the cognitive differences already discussed. What especially characterizes human motivation is not its initiating goals, but rather the indirection and complexity of its approach to those goals. With our superior capacity for temporal integration and our higher level concepts which enable us to foresee a series of causes and consequences, we can make long-range plans by which our ultimate goals are more efficiently approached. We are not restricted to an immediate striving towards the advantages of the moment.

Through complications introduced by social interaction and culture, most of our activities may appear unrelated to primary drives, but our more obvious goals are merely way-stations on the road to satisfying a relatively few simple but universal needs. As to Simpson's criterion of "a sense of values" for differentiating between man and the lower animals, I believe that no one who has had intimate acquaintance with the higher nonhuman primates will question that their actions are also guided by a delicately balanced system of values. The larger and stronger male chimpanzee deferring to his female companion in the division of food, even after the female is pregnant and no longer suitable as a sex partner—the animal "punishing" the misbehavior of his cage-mate and in position to inflict serious injury, but contenting himself with merely nipping him painfully—the chimpanzee refusing to expose himself to the frustration of occasional failure in a difficult problem, although he could get a desirable tidbit 50% of the time by merely continuing to make a simple and easy response—these are but a few of many instances of a finely adjusted hierarchy of values. Like man, the chimpanzee has many values only indirectly related to primary needs, as for food, sex, and knowledge. But man recognizes in almost everything some relevance, however farfetched, to his basic needs, and his



system of values therefore has a greater numerical range and thus a greater complexity of interrelationships. Activities motivated by the primary drives involve the whole intricate organization of human economic and cultural life with the many subgoals which occupy most of our attention. Even the motives of altruism, ethical conduct and the like, are the expression of basic motivations, in us guided by superior intelligence, which we share with the other primates.

# LITERATURE CITED

- FORSTER, M. C. 1935 Temporal relations of behavior in chimpanzee and man as measured by reaction time. I. Simple reaction time. *J. Comp. Psychol.*, 20: 361-383.
- GRETHIER, W. F. 1939 Color vision and color blindness in monkeys. *Comp. Psychol. Monogr.*, 15 (4): 1-38.
- 1940 A comparison of human and chimpanzee spectral hue discrimination curves. *J. Exp. Psychol.*, 26: 394-403.
- HOLLINGWORTH, H. L. 1928 *Psychology; Its Facts and Principles*. D. Appleton and Co., New York.
- JAMES, W. 1890 *The Principles of Psychology*. Henry Holt and Co., New York.
- LORENZ, K. 1937 Ueber die Bildung des Instinktbeegriffs. *Naturwissenschaften*, 25: 289-300, 307-318, 324-331.
- NISSEN, H. W. 1951a Phylogentic comparison, in *Handbook of Experimental Psychology* (Ed. S. S. Stevens), John Wiley and Sons, New York.
- 1951b Analysis of a complex conditional reaction in chimpanzee. *J. Comp. Physiol. Psychol.*, 44: 9-16.
- NISSEN, H. W., JOSEPHINE S. BLUM, AND R. A. BLUM. 1949 Conditional matching behavior in chimpanzee. *J. Comp. Physiol. Psychol.*, 42: 339-356.
- NOER, MARY C. AND H. F. HARLOW 1946 Discrimination of ambivalent cue stimuli by macaque monkeys. *J. General Psychol.*, 37: 165-177.
- RAZBAN, G. H. S. 1933 Conditioned responses in animals other than dogs. *Psychol. Bull.*, 30: 261-324.
- SIMPSON, G. G. 1945 The principles of classification and a classification of mammals. *Bull. American Museum of Natural History*, 85, page 35.
- 1949 *The Meaning of Evolution*. Yale University Press, New Haven, Conn.
- SPENCE, K. W. 1934 Visual acuity and its relation to brightness in chimpanzee and man. *J. Comp. Psychol.*, 18: 333-361.







## THE CULTURAL CAPACITY OF CHIMPANZEE<sup>1</sup>

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THE problem with which we are here concerned has been referred to by Kroeber ('48, p. 69) as "the unknown organic basis of the faculty for culture."<sup>2</sup> What sequence of events in organic evolution was necessary to prepare our presumably anthropoid ancestors for the way of life that uniquely characterises man?

We have approached this question by way of the assumption that man's ancestry includes at some stage, a species which was physically and behaviorally similar to the modern chimpanzee—in a general way, if not in detail.<sup>3</sup> (This assumption is not entirely unreasonable, but

<sup>1</sup> The work reported here has been assisted by grants from the American Philosophical Society, The Samuel S. Fels Fund, and by research grant M669 from The National Institute of Mental Health, U. S. Public Health Service. Footnotes 2, 3, 4, and 6 have been added in response to comments made by W. L. Straus, Jr. in his "concluding remarks" on the symposium.

<sup>2</sup> We are surprised by Straus' comment that "culture" is virtually undefinable, especially in view of his recent statement ('53, p. 262) that culture "implies social inheritance from one generation to another," and that "man, or the genus *Homo*, may then be defined as an animal possessing a culture, for it is this feature that particularly distinguishes him from all other animals." Others use the term in the same way, without making an issue of its definition (e.g.: Kroeber, '48, p. 8, Dobzhansky and Ashley Montagu, '47, p. 587.) Moore and Lewis ('52) have discussed the operational definition of culture at some length; but their product differs from others primarily in its unfortunate interaction with the definition of "hominid." Brief definitions are poor substitutes for thorough discussions, which are plentiful in the literature, and which indicate that most anthropologists use the term "culture" consistently, and know what it means.

<sup>3</sup> This is perhaps ambiguous. We do not assume that man's ancestry includes a form which resembled the chimpanzee more closely than it did the orangutan or gorilla. We merely assume an ancestor of broadly "anthropoid" type, which was enough like the modern chimpanzee to make our study of the latter relevant.

its main virtue is convenience: chimpanzees are available for behavioral research.) We have attempted to estimate the extent to which characteristics essential for culture were already present in this hypothetical, chimpanzee-like ancestor.

Our procedure has involved the intensive study of Viki, a chimpanzee who has spent the first six years of her life in our home and has been treated as nearly as possible like a human child (Hayes, '51, Hayes and Hayes, '50). This approach is necessitated by the fact that the behavior of man or any other animal may be markedly influenced by experience—a fact which is seldom denied but which is, unfortunately, often overlooked in comparative psychology (Harlow, '49; Hebb, '49).

We have given special attention to our subject's social behavior, and particularly to her communicative ability—since communication is the primary prerequisite for culture. We have also been concerned with her

The chimpanzee provides a good "model" for our purpose: it has many of the characteristics that man's ancestors are presumed to have had, and it is not highly specialized, in the sense of being irrevocably committed to a narrow adaptive zone. (The chimpanzee is capable of a variety of modes of locomotion, and can utilize a variety of foods obtained in a variety of ways [Yerkes, '43, p. 15, Yerkes and Yerkes, '29, pp. 213-216].)

It is generally agreed that man's ancestry passed through a 400 gram brain stage and a 50 kilogram body weight stage. Most, though not all students (Straus, '49) consider it likely that man's ancestors were structurally adapted for brachiation, at one stage. One of the purposes of this investigation is to evaluate the possibility that an animal with these structural characteristics could have entered the human, or cultural, adaptive zone. If it could, we see no reason to doubt that it could subsequently have made whatever progressive adjustments this adaptive zone favored—even though such adjustments might involve reversal of earlier adjustments to other adaptive zones.

There is some reason to suppose that the African apes have already undergone considerable reversal of the brachiating specialization. Despite common belief (Straus, '49, Hooton, '42), the Hylobatidae are the only living apes that actually use brachiation as a usual or important mode of locomotion (Yerkes and Yerkes, '29, p. 537, Nissen, '31, p. 34). Although the other anthropoids, including chimpanzee, are "brachiators" in a structural sense, they show this adaptation in very attenuated form, as compared with the Hylobatidae. The large apes may reasonably be thought of as descendants of a siamang-like species, who have long since ceased to be selected for brachiation, and whose brachiating structure has been modified toward a more generally useful form. (This interpretation is supported by consideration of the laryngeal air-sac, which is prominent and possibly functional in the siamang, but small and almost certainly non-functional in the living African apes.)

use of implements, since tool-using is a prominent feature of all known cultures.<sup>4</sup>

It seems conceivable, a priori, that cultural capacity might have developed through evolutionary changes of three general types: 1. changes in gross anatomy, 2. development of special mental abilities, 3. changes in motivational makeup. We will examine each of these possibilities in some detail.

#### CHANGES IN GROSS ANATOMY

*The hand.* It might be supposed that considerable modification of the anthropoid hand would be needed to make it adequate for skillful tool using. However, our data do not support this hypothesis; our subject uses a great variety of tools, and she uses them skillfully and easily enough to be of considerable practical value to her (figs. 1 and 2).<sup>5</sup> The relative shortness of her thumb does not, despite common belief, prevent her grasping small objects between thumb and forefinger (fig. 3). We suspect that another peculiarity of the chimpanzee hand, less often mentioned in the literature, may cause more difficulty. This is the lack of dorsiflexion of the wrist (Straus, '40) which sometimes makes it hard to position a tool properly, after it has been grasped. However, this is not a really serious impediment to tool using. Functional plasticity tends to outweigh structural rigidity. If Viki's dexterity is greater than that observed in most other chimpanzees, the discrepancy is readily understandable in terms of the oft-neglected factor of experience. Most chimpanzees have much less opportunity to develop their manual skill than human children have. Also, it must be remembered that many of the tools we ask chimpanzees to use were designed specifically to fit human hands, and are ill-suited for use by chimpanzees. The chimpanzee hand performs rather, poorly with our shears, for instance; but it would probably operate quite effectively with shears designed to fit it (Kroeber, '48, p. 68).

<sup>4</sup> Invention and construction of tools are important too, of course; however, one of the prime functions of culture is to relieve the average individual of much of the burden of creation, by allowing him to utilize the products of his more capable fellows—as pointed out, e.g., by Hooton ('42, p. xxxix). In particular, six-year-old children need not, and normally do not, invent or construct tools to a practically significant extent. For this reason we are postponing a detailed account of Viki's creative activities to a later and more appropriate date.

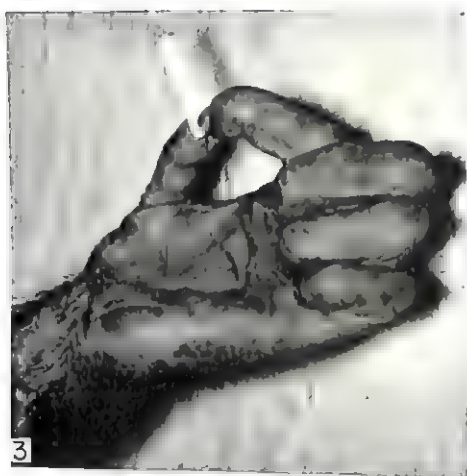
<sup>5</sup> Viki's use of tools is illustrated extensively in a 16 mm, silent film (Hayes and Hayes, '53).



FIG. 1. LIGHTING A CIGARETTE AT 6 YRS.

FIG. 2. TRYING TO PULL A LOOSE TOOTH WITH PLIERS AND MIRROR (6 YRS).





- FIG. 3. HOLDING A CIGARETTE WITH GOOD THUMB OPPOSITION (6 YRS).  
 FIG. 4. CARRYING A HEAVY BOX AT 4 YRS.  
 FIG. 5. DIGGING WITH A SPOON AT 5 YRS.  
 FIG. 6. THROWING A TOY TO KNOCK DOWN A LURE AT 3 YRS.



*Posture.* It has been suggested that modification of the anthropoid posture was the first and most basic step in human evolution, since bipedal locomotion would be needed to free the hands for the use of tools (e. g. Washburn, '50). However, if evolution operates by selection, rather than by foresight, tool using must have appeared first. Only then could the intrinsically inefficient, bipedal mode of locomotion be favored in selection (Bartholomew and Birdsell, '53, p. 482). We seriously doubt that pre-cultural tool using, on an individual basis, would be of sufficient importance to permit bipedalism, and we therefore suggest that cultural tool using appeared when posture was still of the anthropoid type. This seems entirely possible. Most of man's tool using occurs in a sitting position, or a stationary, standing position—neither of which is difficult for chimpanzees (figs. 5 and 6). So far as the transportation of implements is concerned, a chimpanzee can carry small objects in all four extremities while walking quadrupedally, and heavy objects can be carried in both arms, while walking upright—for short distances, at least (fig. 4).<sup>6</sup>

*Speech organs.* The anthropoid lungs, larynx, and mouth have commonly been considered adequate for the production of speech sounds. However, Kelemen ('48) has recently ascribed the absence of speech in chimpanzee to its laryngeal structure. We are not prepared to evaluate Kelemen's anatomical study as such, but we can say with confidence that he is mistaken about its functional significance. It may be true, as he reports, that the chimpanzee larynx is more complex than man's; but it is not true that chimpanzee voice production is more complex than man's, and therefore useless for speech. Chimpanzee vocalization does not differ appreciably from ours in its use of inspired breath or double tones, and the chimpanzee's air sac is not involved in vocalization. Chimpanzees can and do produce a variety of vowel and consonant sounds.

*Brain size.* Controversy over the classification of extinct primates often centers around their cranial capacities. Unless the brain was

<sup>6</sup> Contrary to Straus's interpretation, these two paragraphs have not denied "morphological and physiological changes in [non-neural] parts of the body an important role in the evolution of human behavior." We do deny that changes of this type were prerequisite to the transition from anthropoid behavior to cultural behavior. The omission of certain changes might have led to "men" whose behavior, while quite different from ours, would still be cultural, and in this sense "human."

large enough, the creature presumably could not have been sufficiently "intelligent" to behave like a man, and must therefore have been an ape. We do not know, of course, just how large a brain is "large enough," though Keith ('48, p. 206) has boldly drawn the line at 750 cc. The matter is obscured by the vague manner in which the term "intelligence" is often used. However, if this word is defined operationally in one of the various possible ways, we still have no definite information about its relation to the size of the brain or any of its parts. In the absence of data we venture to speculate as follows: Such processes as forming or retaining an association, perceiving a relationship, drawing an inference, or generalizing a principle, should be relatively independent of sheer mass of tissue. We consider it likely that the quantity of brain is primarily related to a quantitative aspect of its function—specifically to its information handling capacity. One of the most distinctive tasks imposed upon the human brain by man's cultural way of life is the assimilation and storage of a tremendous amount of information. On the other hand, the chimpanzee's 400 gram brain seems to be fully capable of handling all the useful information likely to be encountered directly by the individual. From this point of view, an increase in the size of the anthropoid brain would be of no advantage to its possessor, so long as he continued to lead a non-cultural existence. We suggest the possibility that most of the fourfold increase in cranial capacity, from anthropoid to man, took place after the appearance of culture and language, and therefore after primate behavior had become essentially human.<sup>7</sup>

#### SPECIAL MENTAL ABILITIES

The second type of evolutionary change which may, conceivably, have led to the appearance of culture, is the development of complex patterning in the fine structure of the brain, which would provide special mental abilities not adequately developed at the anthropoid level. These micro-anatomical details would be inaccessible not only to paleontological methods, but also to present histological techniques, so this kind of structural evolution could be known only by inference from behavioral data (Lashley, '47).

<sup>7</sup>Thorndike ('27, p. 415) has suggested that the innate component of intelligence is nothing more than the number of potential associative bonds available in the brain. We have made one abortive attempt to deal with information capacity experimentally, but there is still considerable doubt whether this will ever be practical (Hayes, Thompson, and Hayes, '52).

This brings us to the question of whether chimpanzees are deficient, as compared with man, in their neurological capacity for behavior which may be characterized as, for instance, abstract, symbolic, conceptual, relational, insightful, or foresightful. These concepts appear to have their sources in the complex behavior (or introspection) of sophisticated humans. This may account for the difficulty of defining them in terms of experimental operations applicable to non-cultural, non-linguistic, and uneducated subjects (e. g., Seward, '48, p. 280).

Man does not display these "higher mental functions" in a vacuum, but only in the context of skills and information which have been acquired through experience. A primate who has not acquired the same skills and information can hardly be expected to display these functions in the same form as man. If a primate's background of experience is sufficiently restricted, he may fail to display any "higher functions" in any form whatever—simply because of his lack of skills and information and regardless of the detailed structure of his brain. There have been only a few experimental studies which bear directly on this question, but they tend to support the hypothesis that "higher mental abilities" are acquired rather than inherited.

Tasks which involve the integration of events separated by an interval of time are sometimes said to require special "symbolic processes," and it is known that such tasks are extremely difficult for naive chimpanzees (Hallowell, '50, p. 165; Yerkes, '43, p. 188). Several studies have shown, however, that this difficulty may be eliminated by prior experience with simple discrimination-learning problems (Harlow, '44; Hayes and Thompson, '53; Riesen, '40).

It was once possible to suppose that learning by observation, as contrasted with direct experience, depended on some faculty which was confined primarily to man. Here again, however, an adequate background of experience has been found to make such learning very easy for other primates (Harlow, '44; Hayes and Hayes, '52).

In short, when the factor of experience is considered, there is no clear evidence that chimpanzees are deficient in any hypothetical, higher mental faculties. Furthermore, it may be questioned whether these special abilities actually exist, as such, even in man. We are inclined to favor Thorndike's hypothesis that "in their deeper nature the higher forms of intellectual operation are identical with mere association or connection forming, depending upon the same sort of physiological connections but requiring *many more of them*." (Thorndike et al., '27,

p. 415). We suggest that the "higher mental functions" observed in man are more nearly results of culture than causes of it.

#### MOTIVATIONAL MAKEUP

The third and last type of evolutionary development concerns the neural mechanisms which cause an animal to engage in various kinds of activity (Harlow, '53). These mechanisms are presumably micro-anatomical and inaccessible to direct observation but may be inferred from behavior. We are not particularly interested in the drives which cause an animal to eat, drink, and reproduce, but rather in the play drives—the innate tendencies toward behavior which serves no immediate, practical purpose. Such behavior has survival value because it provides opportunity for the acquisition of skills and information which may later be useful in the solution of practical problems. To avoid any irrelevant connotations of the word "play" (Beach, '45; Schlosberg, '47) and to indicate explicitly the significance of this phenomenon, we offer the alternative term, "experience-producing drives."

Cultural living, as we know it, requires an adequate background of experience in at least two broad areas: mechanical and social. The first is essential to the technological aspect of culture and the second to communication and cooperative enterprise.

*Mechanical play.* The chimpanzee resembles man very closely in mechanical interest. Our subject, Viki, spends a large part of her time playing with tools, toys, and household equipment, as well as with more primitive materials, such as sand, sticks, and water. This extensive mechanical play, coupled with the dexterity mentioned earlier, permits the chimpanzee to develop a very respectable amount of mechanical ability. It is our belief that no further evolution would be necessary to prepare the chimpanzee for the tool-using side of cultural life.

*Social and communicative play.* Chimpanzees also resemble man quite closely in preference for social play. Viki likes simple games which involve tickling, wrestling, chasing, and teasing; and it seems likely that such communicative ability as she has was acquired largely in the course of such play. However, she is markedly deficient in one type of drive which is very prominent in man—the drive toward specifically communicative and linguistic play.

This type of play appears as babbling in the human child, early in the first year of life, and provides extensive practice in the motor skills



of producing and combining speech sounds. During the next few years, after the child has learned the elements of speech, he takes great interest in learning new words—most of which have no practical value for him at the time, though they may be useful later. For the rest of the child's life, a large proportion of his speech satisfies no more immediate, practical need than that for self expression.

In the infant chimpanzee, however, vocal play is almost completely absent. During her first five months, Viki babbled enough to show that her vocal apparatus was capable of producing a variety of vowel and consonant sounds; however, she did much less of this than human infants do, and the activity did not persist nearly so long (Hayes, '51, p. 63).

After their first year, many chimpanzees engage in a type of sound-producing play which is somewhat similar to babbling; however, the sounds are produced by mouth movements only, without use of the larynx, and usually without use of the lungs. Some of these sounds closely resemble the "clicks" which form a part of certain human languages. Viki has produced only six of these sounds, and has shown no tendency to combine them in groups. They could thus provide only a very limited potential vocabulary.

Viki readily imitates our production of her mouth sounds and learns meanings which we assign to them. She can thus ask for a drink by saying "ch" (with the German pronunciation, as in *Ich*), or for a cigarette by saying "tsk," or for a ride in the car by clicking her teeth together. However, unlike the human child who has just begun to speak, Viki uses her words only for the practical purpose of getting what she wants. She does not engage in purely sociable conversation, or egocentric expression. She does not even use her words for practical purposes, if she can show us what she wants without them. When she wants a cup of cocoa, for instance, she silently leads us to the kitchen and hands us the ingredients. Only if we refuse to be led and stubbornly ask, "What do you want?" does she say "ch."<sup>s</sup>

We suggest that the most important step in the evolution of modern man from an anthropoid ancestor was an increase in the experience-producing drives relevant to the skills of communication. Others have hypothesised that apes do not talk because they have nothing to say (Kroeber, '28, p. 329). This seems to us like an inadequate reason—

<sup>s</sup> Some of Viki's vocal behavior is illustrated in a 16 mm, sound film (Hayes and Hayes, '50).



it does not keep people from talking. Furthermore, we have found that Viki often does have things to say. We contend that apes do not talk because unlike man, they have no inclination to talk when there is nothing to be said.

We have, in the past, suggested that chimpanzees may be innately deficient in some neurological mechanism which provides the capacity to learn language (Hayes, '51, p. 66). We still consider it conceivable that if a chimpanzee and a human child both had the same language experience, the chimpanzee might learn much less language. However, we now recognize that such speculation is meaningless, so far as available operations are concerned. It is impossible to coerce a chimpanzee into the kind and amount of language practice that the human child gets spontaneously. Since the known difference in motivation accounts for the observed difference in attainment, there is no point in postulating an unknowable difference in capacity.

#### COMMUNICATION AND EARLY CULTURE

The simple beginnings of culture would require only a little skill in communication—perhaps about as much as chimpanzees already have (Kroeber, '48, p. 223). It is important, in this connection, to note the difference between the invention and use of tools, on the one hand, and tool culture on the other. The importance of communication increases as the probability of an invention decreases. Invention of the wooden club, or the stone-used-as-a-missile, would probably occur in a large majority of isolated, individual chimpanzees, under appropriate circumstances, and would thus be independent of culture. The stone-tipped spear, however, would probably be invented very seldom, and would be available to a whole population, in successive generations, only if the methods of manufacture and use could be communicated. The chimpanzee's ability to learn by imitation would appear to make this possible—at least for simple tools and techniques.<sup>9</sup>

Another function of communication in culture is the facilitation of cooperative enterprise. Chimpanzees are capable of considerable communication which could serve for directing, instructing, commanding, or soliciting. Crawford ('37) has demonstrated cooperative behavior in the setting of a laboratory problem, and Viki commonly displays it spontaneously. She often requests our help with things which she cannot do, or is forbidden to do, or afraid to do, by herself.

<sup>9</sup> Viki's imitative ability is illustrated in a 16 mm, silent film (Hayes and Hayes, '52a).

The first method she used was the simple one of leading us where she wanted us to go. More recently, she places our hands on the objects she wants us to manipulate and often moves our hands in a manner suggesting the action to be performed. For instance, if she wants to go outside, she leads us to the drawer where the door key is kept and places our hand on the drawer pull. If we don't open it promptly, she gives our wrist a tug. When the drawer is open, she puts our hand to the key, and when we grasp it, she moves our hand to the key hole. If we continue to lag, she moves our hand till the key enters the key hole and finally twists our wrist to indicate the unlocking movement. (She knows how to unlock the door for herself, of course, but is not permitted to.)

Viki makes relatively little use of gestures of the hand alone, without contacting an object or person. She often points to things she wants, when they are near by and could be touched if that were allowed; but she seldom points to the door across the room, for instance, though she responds appropriately when we do so. She uses movements of her own hands to indicate an activity only rarely—as in the case where she wanted to help with the ironing but was forbidden to touch the iron. She moved her empty hand back and forth above the ironing board, apparently to show what she wanted.

This kind of communication may be said to involve "iconic signs," whose meanings are related in an obvious and logical way to their physical character. We have observed some behavior in Viki which suggests that chimpanzees may readily convert such signs into "symbols," whose meanings have an essentially arbitrary relationship to their physical character. When Viki was very young, we never took her for a ride in the car without taking some spare diapers along. As a result, she invented the device of asking for a ride by bringing us a handful of diapers from the bathroom. Later, she no longer wore diapers, but there were still some in the bathroom, and she still brought them out when she wanted a ride. When we eventually disposed of the non-functional diaper supply, Viki asked for a ride by running into the bathroom and coming out with a handful of Kleenex tissues—which bore only a faint resemblance to diapers. These tissues had never had any direct connection with rides, and by this time Viki had quite likely forgotten how the whole thing started. Except for its history, this would now appear to be communication by means of an arbitrary convention developed by the chimpanzee.

Viki commonly employs a particular type of vocalization in combination with her non-linguistic communication. This is a hoarse "ah," which serves to attract attention, and to indicate "asking," in a very general sense. We have observed a few other chimpanzees using this sound in the same way; but there appear to be very large individual differences in the ease with which it is produced. Some seem to do it spontaneously, while others fail to do it even with extensive training. This sound, unlike the chimpanzee's vocal expressions of emotion, is produced at will (Hayes, '51, p. 66) and could, conceivably, provide the starting point for development of spoken language.

We estimate that chimpanzees are capable of enough communication to permit several kinds of cooperative enterprise which might be typical of very primitive culture. An individual could go and get one or more others and bring them to a place where there was something to be done: a heavy load to be transported, a large animal to be attacked, or a good supply of fruit to be picked. If the nature of the task were not immediately apparent to the newcomer, he might be shown what was wanted. If he did not understand the technique to be used, he could ask for a demonstration. If he were reluctant to work, he might be coerced.

Chimpanzees could probably communicate well enough for some kinds of organized, group hunting: they might, for instance, be able to surround a herd of animals and stampede them over a cliff. We doubt, however, that they could arrange for certain individuals to wait in ambush while others drove the quarry to them. Their communication would probably be inadequate to deal with events remote in time or space.

If chimpanzees have this much cultural capacity, the question naturally arises, "Why don't they have culture?" There are several possible answers. One is that perhaps they do have some. We know relatively little about chimpanzee behavior in the wild (Nissen, '31) and cultural factors may well be involved in some of it. Another possibility is that culture appears only in the presence of excess capacity. Or it may depend on some unrecognized factors which we have not considered.

However, we tend to prefer the hypothesis that chimpanzees lack culture because they are adequately adapted to their environment without it (Nissen, '31, p. 104). Their mortality is probably due primarily to infectious disease (Schultz, '50, p. 51) and would not be reduced by

the techniques of a primitive culture. Food shortage, predators, or a rigorous climate could be combatted by simple cultural means; but these do not appear to be important factors in chimpanzee survival.

#### CONCLUSION

In summary, we hypothesize that modern man evolved from an anthropoid ancestor by way of the following sequence of events.

1. Due to migration or changing climate, a population of anthropoids encountered an environment in which cultural behavior had greater survival value than it has in the ecology of present anthropoid species. (This probably involved a shift from vegetable to animal food, which would present no serious difficulty. Viki eats a considerable amount of eggs, fish, and meat, including small lizards which she catches.)

2. In response to the new environmental pressure, a simple, non-linguistic culture developed, which provided primitive tools and techniques for obtaining food, or protection from predators or climate.

3. In this cultural setting, language acquired a value it did not have before and began to develop on the foundation of a few sounds such as chimpanzees are able to use. With the appearance of language, selection occurred in favor of individuals with strong drives toward vocal and linguistic play, so that successive generations learned more language, and learned it more easily.

4. Finally, as the linguistic culture became more complex, larger information capacity became advantageous, and selection for large brains began. This selection probably operated on the growth pattern, producing a rather generalized fetalization (Keith, '48, p. 197; Schultz, '50, p. 46), with mature brain size as the basis of selection, and jaw size, head balance, etc., as incidental, correlated features.

It will be noted that the much discussed change in posture does not appear in this behaviorally oriented schema. The recent discovery of the pelves of South African ape-men (Broom, '50; Dart, '49) suggests that bipedal locomotion preceded brain enlargement in the evolution of man. However, it does not follow that upright posture was the first or most basic step in human evolution (Washburn, '50). The present analysis shows that it is a secondary character of only moderate importance. We agree with Kroeber's suggestion ('48, p. 68) that it could have been omitted completely, without seriously altering the basic outlines of human evolution.

## LITERATURE CITED

- BARTHOLOMEW, G. A., JR. AND J. B. BIRDELL 1953 Ecology and the proto-hominids. *Am. Anthrop.*, 55: 481-498.
- BEACH, F. A. 1945 Current concepts of play in animals. *Amer. Nat.*, 79: 523-541.
- BROOM, R. AND J. T. ROBINSON 1950 Notes on the pelvis of the fossil ape-men. *Am. J. Phys. Anthrop.*, n. s. 8: 489-494.
- CRAWFORD, M. P. 1937 The cooperative solving of problems by young chimpanzees. *Comp. Psychol. Monog.*, 14, No. 68.
- DART, R. A. 1949 Innominate fragments of *Australopithecus prometheus*. *Am. J. Phys. Anthrop.*, n. s. 7: 301-333.
- DOBZHANSKY, T. AND M. F. ASHLEY MONTAGU 1947 Natural selection and the mental capacities of mankind. *Science*, 105: 587-590.
- HALLOWELL, A. I. 1950 Personality structure and the evolution of man. *Am. Anthrop.*, 52: 159-173.
- HARLOW, H. F. 1944 Studies in discrimination learning by monkeys: II. Discrimination learning without primary reinforcement. *J. Gen. Psychol.*, 30: 13-21.
- 1949 The formation of learning sets. *Psychol. Rev.*, 56: 51-65.
- 1953 Mice, monkeys, men, and motives. *Psychol. Rev.*, 60: 23-32.
- HAYES, C. 1951 *The Ape in Our House*. Harper, New York.
- HAYES, K. J. AND C. HAYES 1950 Vocalization and Speech in Chimpanzees, (16 mm, sound film.) *Psychological Cinema Register*, State College, Pa.
- 1951 The intellectual development of a home-raised chimpanzee. *Proc. Amer. Phil. Soc.*, 95: 105-109.
- 1952a Imitation in a home-raised chimpanzee. (16 mm, silent film.) *Psychological Cinema Register*, State College, Pa.
- 1952b Imitation in a home-raised chimpanzee. *J. Comp. Physiol. Psychol.*, 45: 450-459.
- 1953 The mechanical interest and ability of a home-raised chimpanzee. (16 mm, silent film.) *Psychological Cinema Register*, State College, Pa.
- HAYES, K. J. AND R. THOMPSON 1953 Non-spatial delayed response to trial-unique stimuli in sophisticated chimpanzees. *J. Comp. Physiol. Psychol.*, 46: 498-500.
- HAYES, K. J., R. THOMPSON AND C. HAYES 1953 Concurrent discrimination learning in chimpanzees. *J. Comp. Physiol. Psychol.*, 46: 105-107.
- HEBB, D. O. 1949 *The Organization of Behavior*. Wiley, New York.
- HOOTON, E. 1942 *Man's Poor Relations*. Doubleday, New York.
- KEITH, A. 1948 *A New Theory of Human Evolution*. Watts & Co., London.
- KELEMEN, G. 1948 The anatomical basis of phonation in the chimpanzee. *J. Morphol.*, 82: 229-256 (reprinted in *Yearbook Phys. Anthrop.*, 1948, 4: 153-180.)
- KROEBER, A. L. 1928 Sub-human cultural beginnings. *Quart. Rev. Biol.*, 3: 325-342.



- 1948 *Anthropology*, Harcourt Brace, N. Y.
- LASHLEY, K. S. 1947 Structural variation in the nervous system in relation to behavior. *Psychol. Rev.*, 54: 325-334.
- MOORE, O. K. AND D. J. LEWIS 1952 Learning theory and culture. *Psychol. Rev.*, 59: 380-388.
- NISSEN, H. W. 1931 A field study of the chimpanzee. *Comp. Psychol. Monog.*, 8, No. 1.
- RIESEN, A. H. 1940 Delayed reward in discrimination learning by chimpanzees. *Comp. Psychol. Monog.*, 15, No. 5.
- SCHLOSBERG, H. 1947 The concept of play. *Psychol. Rev.*, 54: 229-231.
- SCHULTZ, A. H. 1950 The specializations of man and his place among the catarrhine primates. *Cold Spring Harbor Symposium*, 15: 37-53.
- SEWARD, J. P. 1948 The sign of a symbol: a reply to Professor Allport. *Psychol. Rev.*, 55: 277-296.
- STRAUS, W. L., JR. 1940 The posture of the great ape hand in locomotion and its phylogentic implications. *Am. J. Phys. Anthropol.*, 27: 199-207.
- 1949 The riddle of man's ancestry. *Quart. Rev. Biol.*, 24: 200-223.
- 1953 in TAX, S. (Ed.) *An Appraisal of Anthropology Today*. Univ. of Chicago Press.
- THORNDIKE, E. L., E. BREGMAN, M. COBB AND E. WOODYARD 1927(?) The Measurement of Intelligence. Bureau of Publications, Teacher's College, Columbia Univ., N. Y.
- WASHBURN, S. L. 1950 The analysis of primate evolution with particular reference to the origin of man. *Cold Spring Harbor Symp.*, 15: 67-77.
- YERKES, R. M. 1943 *Chimpanzees*. Yale Univ. Press, New Haven.
- YERKES, R. M. AND A. YERKES 1929 *The Great Apes*. Yale Univ. Press, New Haven.





## CLOSING REMARKS

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I BELIEVE that I am correct in stating that the peak of research on the nonhuman primates in this century was reached during its third and fourth decades. During the last fifteen or more years, however, the output of such studies has fallen off to a marked degree. The reason for this I do not know. Perhaps it is due to the war. Whatever the reason, however, the number of workers now actively engaged in primate research is almost pitifully small. The response evoked by this symposium leads me to hope that it may signal the beginning of a revival; for, although I admit to something more than a slight prejudice, I know of no aspect of anthropology that is likely to yield richer dividends to the investigator.

I am glad to note that Dr. Hooton agrees in essence with what I said at last year's Wenner-Gren international symposium about the present status of our knowledge of primates and about the important gaps that remain to be filled. He has, however, stated the case for extensive and intensive studies of nonhuman primates far more eloquently and more effectively than I possibly can.

I heartily endorse his statement about the pressing need for a broad and sound knowledge of nonhuman primates when reconstructing and interpreting the fossil remains of man and other primates. I would go even further, however—and I am sure that he will agree with me—and stress the imperative need of comparing fossils with large series of existing primates, utilizing biostatistical methods. There has been far too much reliance on that more facile method which a former mentor of mine used to call "anatomical appreciation." I know that I may be stepping on tender toes when I say this; nevertheless, I believe that too

much of what has been written about the *Australopithecines* falls into the latter category. And many studies of primate teeth, as Dr. Hooton has rightfully emphasized, furnish yet another important example.

Dr. Hooton has also emphasized the paucity, indeed the virtual absence, of genetic studies of nonhuman primates—studies that would, with little doubt, help elucidate some of the problems of human evolution. The obstacles to such studies are of course great, but so would be the rewards. The cooperation of primatologists, geneticists, and directors of zoological parks could scarcely fail to reap a rich harvest.

The paleontological papers of Dr. Jepsen and Dr. Patterson cannot help but impress upon us the important fact that the geological history of the primates is an extremely long one. As Dr. Jepsen has noted, only three of the living mammalian orders—the marsupials, the insectivores, and the carnivores—have, in our present knowledge, longer histories. Man is a terminal product of some 65 million years of primate evolution, and if we are really to understand him, we must take due cognizance of what has gone before. In this, as will again be noted later, Dr. Davis and myself see eye to eye. The whole gamut of primate evolution, from the early prosimians of the North American Paleocene onward, has undoubtedly left its mark on man as we know him today. In the past—indeed, even at the present time—too many students of human evolution have focussed their attention too closely or even exclusively on those animals that appear to stand nearest to man—that is, on the anthropoid apes, and particularly on the great apes—with resulting myopia and scotomata. The consequences of such a limited outlook have become all too evident in some evolutionary controversies. Although the geological history of the primates exhibits many irritating gaps, some of them are gradually being filled in. Indeed, certain recent discoveries have shed new light upon man's history: light that is in some respects quite unexpected in its nature. Yet many important problems of primate evolution remain for elucidation. To give but an incomplete list, there are the relationship of the tupaoids to the lemuroids and tarsoids, the question of a tarsoid origin of the simian primates, the history of the platyrrhines, the evolutionary relationships of the existing catarrhine groups, and, last but not least, the nature and the zoological position of the *Australopithecines*.

Some of these problems have been discussed by Dr. Patterson. He has made it clear that paleontology cannot yet speak with authority on the taxonomy and phylogeny of the primates. The poverty of

primate paleontology as compared with that of certain other mammalian orders is undoubtedly to a large degree a reflection of the habits and habituses of primates, which do not favor preservation of these animals as fossils. Notwithstanding, as Dr. Patterson points out, paleontology is in a position to make certain reasonable suggestions. It is impossible for me even to note, much less discuss, all of the interesting points that have been raised in his stimulating paper; so I will confine myself to a few that seem particularly pertinent.

Dr. Patterson is inclined to agree with Barth that in early Tertiary times the differences between lemuroids and tarsoids were not very important. This might be interpreted as indicating a late separation of the two groups, a view that seems recently to have gained in popularity; but, as Dr. Patterson notes, the history of the so-called prosimians is far from clear.

I am extremely interested in Dr. Patterson's appraisal of those late Eocene and early Oligocene catarrhines termed, respectively, *Amphipithecus*, *Moeripithecus*, *Parapithecus*, *Propliopithecus*, and "*Kansupithecus*," all known only by their lower jaws. As he states, they were "probably of the greatest importance in primate history"; but he is only being realistic when he advocates that they be listed simply as Catarrhina (or Anthropoidea) *incerta sedis*. To them might also be added *Oreopithecus*, with which Dr. Patterson has dealt so illuminatingly, and *Apidium*. Various theories, some of them smacking of dogmatism, and in general not warranted by the meager evidence that the specimens provide, have been spun around these fragments. It is better to admit, as Dr. Patterson intimates, that the origins and early history of the catarrhines are still largely shrouded in mystery.

Dr. Patterson has shown us two diagrams of primate phylogeny, one by Dr. A. H. Schultz and one by himself. That these diagrams, each by an outstanding student of primates, can differ so strikingly in so many important points, is highly significant. It emphasizes the fact that in the present state of our knowledge it is quite possible to arrive at very different interpretations of primate history. It can scarcely be doubted that future paleontological discoveries will bring about important and perhaps even startling changes in our concepts of primate phylogeny.

I fully endorse Dr. Patterson's appraisal of the available evidence as indicating that "extreme brachiation was a very late event in catarrhine evolution." But when he suggests that preadaptation to brachia-

tion was peculiar to the pongid or hominoid stock, which gave rise to the existing anthropoid apes and man, I cannot quite go along with him. I do not intend to discuss the moot question of whether there was a brachiating stage in man's ancestry; for this symposium is primarily dedicated to the nonhuman primates. Furthermore, as I have pointed out elsewhere, the matter of semantics is involved, in that the term "brachiation" does not mean the same thing to all students. However, I wish to note that bimanual progression is not limited, among the catarrhines, to the pongids. Some of the living cercopitheine monkeys swing by the arms on occasion and hence might well be regarded as primitive brachiators; and the semnopitheine monkeys, especially *Colobus*, are even more addicted to this type of locomotion. Thus I submit that the penchant for occasional or moderate arm-swinging, or call it "brachiation" if you will, probably was common to the whole of the catarrhine stock rather than restricted to the pongid or hominoid radiation as Dr. Patterson suggests. That acceptance of this concept might alter one's views on the phylogeny of the catarrhines, surely need not be emphasized here,

I wish that there were time to discuss Dr. Davis' paper at length, for it is full of stimulating ideas. He rightly insists that the central problem of comparative anatomy, and of historical biology in general, is to explain—rather than simply to describe—the events of organic evolution. His emphasis on genetics and morphogenetic fields is in line with the concepts of the newer comparative anatomy. Dr. Davis believes that mutations having relatively major phenotypic effects have played a part in evolution. This belief, as he realizes, represents a scientific heterodoxy with which, however, I am personally inclined to agree. His insistence that structure cannot be divorced from function, and that comparative anatomy is sterile without this dual emphasis, represents a repudiation of the still dominant Gegenbaurian concept of comparative anatomy—a repudiation to which I heartily subscribe. Dr. Davis has presented a method for the sorting out of morphological characters into categories, separating the phylogenetically old from the phylogenetically new. Although this procedure is scarcely new in comparative anatomy, yet that some such evaluation is necessary and needs reemphasis is of course obvious. But when it comes to labelling characters as "heritage" or "habitus" traits, I can only repeat what I said in 1949: "This method might be valid were we able, with any degree of conviction, to separate characters into such distinct categories. . . . Furthermore, it is



exceedingly doubtful whether such a separation is justifiable, if for no other reason than that it remains to be proven for any character that it is not in some way adaptive. Even assuming that there is such a truly fundamental distinction, there is every reason to believe that gene complexes underlie both such kinds of characters." Finally, Dr. Davis' emphasis on the importance of studying the treeshrews and the generalized insectivores in attempting to understand human evolution is in line with what has already been said. Students of man's evolution cannot stop with man, nor even with the primates. The whole of mammalian history, even of vertebrate history, has left its mark upon him. Hence the anthropologist needs a broad comparative point of view.

Aside from the light that they cast on existing forms, the papers of Drs. Schuman and Brace, Dr. Tappen, and Dr. Erikson in this symposium provide data of great value in the interpretation of the remains of fossil primates in general; they also are of particular value in interpreting the vestiges of human evolution.

The detailed study of Drs. Schuman and Brace of the variability of the permanent teeth in a representative population sample of the Liberian chimpanzee, with its valuable statistical analysis, constitutes a truly major contribution. As Dr. Hooton has pointed out, and as I have noted elsewhere, sweeping phylogenetic conclusions derived from dental morphology have all too often been based upon inadequate knowledge of dental variability, whether this variability be intrageneric, intra-specific, or at a lower taxonomic level. Primate taxonomy, whether one likes it or not, is, largely because of paleontological necessity, primarily a dental one. Yet, detailed knowledge of normal dental variability in primates is shockingly inadequate. Thus, as I have said elsewhere, and which I now repeat with apologies, "it is not improbable that undue emphasis has often been placed upon slight differences in dental morphology, with consequent taxonomic or phylogenetic interpretations that would not have been drawn had more information regarding the dental variability of the involved form or forms been available." The study of Drs. Schuman and Brace, the importance of which can scarcely be overstressed, helps fill in one of the many yawning gaps in our knowledge of primate dentitions; in doing so, it demonstrates the high degree of dental variability that can occur within a homogeneous primate population—a demonstration which, it is to be hoped (though perhaps I am overoptimistic), may serve as a rein upon unbridled odontological speculation. It is also to be hoped that this study will

provide a stimulus for further studies of this sort. It would be particularly instructive to compare Drs. Schuman and Brace's group of chimpanzees with that other large and homogeneous sample from a totally different locality belonging to the Todd Collection of Western Reserve University.

Dr. Tappen's split-line studies of the orientation of Haversian systems within the skulls of representative primates is an example of the application of one of the newer techniques to a dynamic analysis of the skeleton—a type of approach for which anthropology is largely indebted to Dr. Washburn. Despite the limitations admittedly inherent in this particular technique—namely, its restriction to the more external details of bony structure—it has already yielded basic information respecting at least some of the factors involved in the forms of bones, and the contributions possible by this method are almost innumerable.

I have followed Dr. Erikson's long-term study of the New World monkeys with great interest; for the platyrrhines represent an important and relatively neglected primate group. Although almost nothing is known of their geological history, as Dr. Jepsen has pointed out, there nevertheless is little or no reason to doubt that they have long pursued their own course of evolution quite independent of the catarrhines and that the numerous, intriguing similarities between the two simian groups represent autonomous developments. Because of these striking parallels the platyrrhines assume a somewhat strategic position for providing data that can aid in elucidating the phylogenetic relationships of catarrhine groups. Detailed knowledge of platyrrhine morphology and its relations to ecology and physiology, both locomotor and otherwise, will certainly aid in the analysis and interpretation of the several and somewhat diverse types of brachiation that have evolved, apparently quite independently, in various Old World simians. Indeed, it may well throw light upon that important and vexed question, already noted above: "What role, if any, did brachiation play in the evolution of man?" As Dr. Erikson notes, the majority of studies of human phylogeny have been too exclusively restricted to men and anthropoid apes and too narrowly focussed on the skeleton, especially on the skeleton of the head. From the point of view of primate paleontology, his studies are of particular significance for any analysis of the functional characters of postcranial skeletal remains. Also of great importance to students of human phylogeny is the emphasis that Dr. Erikson places, and rightly so, I believe, upon the necessity of truly recognizing the existence of the

phenomenon of parallelism. And, finally, which should provide anthropologists and paleontologists with food for thought, there are the disharmonies and puzzles that he notes—such disharmonies and puzzles as the association of seemingly similar morphological patterns with very dissimilar habituses, and the reverse. Although his particular analysis relates to New World simians, it is obvious that this type of study is also quite applicable to the simians of the Old World.

It is beyond my capacity to analyze critically the papers of Drs. Carpenter, Nissen, Harlow, and Hayes. But there are several comments that I would like to make.

Dr. Carpenter's paper underlines the importance of field studies of nonhuman primates, like those that he has already made on howlers, on spider monkeys, on macaques, and on gibbons, like that of Dr. Nissen on chimpanzees and like that of Dr. Zuckerman on baboons. I can only echo Dr. Hooton's plea for more studies of the social life of contemporary nonhuman primates in natural environments; and I likewise deeply deplore the virtual cessation of such studies. For, like Dr. Hooton, I am convinced that studies of this sort are more likely to illuminate the origins and evolution of human social organization and behavior than are studies of "primitive" or "uncivilized" human groups. And I say this without intending at all to deny the value of the latter type of study.

The papers of Drs. Nissen and Harlow stress the importance of non-homeostatic and, at times, apparently purposeless motivation in primate behavior—such things as play, exploration, and curiosity. This may possibly be something that is essentially peculiar to primates, at least in the degree of its development. To express it in the language of a layman, it is what I like to call the "cussed curiosity" of primates, at least of simian primates. I strongly suspect that this "cussed curiosity" is even more highly developed in Old World simians than in New World simians, although I cannot support my suspicion by controlled observations. If this is actually true, it may well explain why it fell to the lot of the Old World simians to produce a cussedly curious, cantankerous, highly individualistic, and successful creature such as man, with all of his appurtenances that collectively go to make up the phenomenon which passes under that vague term, "culture."

Psychobiological studies, such as those discussed in this symposium, prove, quite as definitely as morphological ones, that man is a primate and, more particularly, a catarrhine primate. But, effective as they are

in providing knowledge of the raw materials that go to make up human behavior, they still fall short of explaining that great behavioral difference between man and those animals that Dr. Hooton has so pungently termed "man's poor relations." I was about to say that the difference is one of culture; but "culture" is a word that has been bandied about and which is difficult to define, as the paper of Dr. and Mrs. Hayes so clearly demonstrates. Man's prime behavioral peculiarity and his greatest distinction resides in the fact that he is a time-binder and a tool-maker. The former may be merely a matter of degree when comparison is made with other animals, but the fact remains that man is peculiar in the extent to which he lives in the three dimensions of time. It is this peculiarity that gives rise to his remarkable degree of foresight or anticipation which is perhaps best expressed in tool-making, to use this term in its broadest sense. And it is tool-making—not tool-using, as the Hayeses seem to believe—that represents the greatest distinction of man. It is the expression of the capacity of men for making—to borrow Dr. Nissen's words—"long-range plans by which our ultimate goals are more efficiently approached." The actual basis of this human trait remains to be determined. That it is largely neurological, there seems little doubt. Yet to deny morphological and physiological changes in other parts of the body an important role in the evolution of human behavior as the Hayeses would seem to do, strikes me as unrealistic and naive. It is more than difficult to believe that non-neural structures do not also play a role in the determination of behavior. Thus, as I have stressed elsewhere, the happy combination of an adequate brain and an adequate hand undoubtedly played a major role in determining the course of human evolution.

The hypothesis of Dr. and Mrs. Hayes regarding the origin and early evolution of human behavior is an interesting one, which, at the present time, can be neither proved nor disproved. Their argument is beclouded, however, by resort to that vague term, "culture," which, as Dr. Hooton has noted, is virtually undefinable.<sup>1</sup>

<sup>1</sup> During the discussion at the Wenner-Gren Foundation International Symposium on Anthropology held in June, 1952, I suggested that man may be defined as "an animal possessing a culture" (see *An Appraisal of Anthropology Today*, 1953, pp. 262-264). Subsequently, it has been amply demonstrated that the term "culture," even in its application to present-day human groups, is used inconsistently by anthropologists and without general agreement as to its precise meaning. The recent reviews of Kroeber's *The Nature of Culture* and Kroeber and Kluckhohn's *Culture: A Critical Review of Concepts and Definitions* by



It is far from my intention to belittle the importance of the truly fine contributions that have resulted from psychological studies of chimpanzees. Nor do I wish to impugn Dr. and Mrs. Hayes' interesting study of Viki. But it should always be remembered that it is unwise to place undue emphasis upon an organism that may well be, insofar as the evolution of man is concerned, deviant. The assumption of Dr. and Mrs. Hayes that "man's ancestry includes, at some stage, a species which was physically and behaviorally similar to the modern chimpanzee—in a general way, if not in detail," is, in the light of present knowledge, certainly open to serious question. That the chimpanzee is adapted to a peculiar mode of life, involving morphological and physiological specializations of a high order, is not to be seriously doubted. And that there consequently are accompanying behavioral specializations must be taken for granted. The concept of a "chimpanzee" stage in human evolution is, to put it mildly, a bit atavistic—it is downright Haeckelism.

I have found it somewhat disturbing to hear the psychologists use such terms as "phylogenetic scale," "phylogenetic level," and "higher" and "lower." It is difficult for me to believe that they use these terms seriously. In any case, we had best abandon such terms. For we shall never truly understand human evolution if we think in terms of a *scala naturae*—no more so than if we think in terms of a "great chain of being."

In closing, I can only emphasize that anthropology is by nature a highly eclectic science. It is far too broad in scope to be adequately mastered by any one person. Therein lies its strength, for it serves as a focal point for workers in many fields. The symposium just completed amply attests to this.




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Leslie A. White and Joseph H. Greenberg, and of *Anthropology Today and An Appraisal of Anthropology Today* by Wilson D. Wallis (*Am. Anthropologist*, vol. 58, no. 3, June 1954) make this quite evident. The term "culture" remains particularly "vague" and "virtually undefinable" when applied to the comparative study of behavior within the order Primates.



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## THE INTERPUPILLARY DISTANCE IN MENTALLY DEFECTIVE PATIENTS

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### INTRODUCTION

THE interpupillary distance is a measurement which has been widely used in physical anthropology. It shows considerable variation in different populations; the eyes of Africans are more widely spaced than those of Europeans, for example. The measurement is likely also to be of clinical interest because, among defectives, a large number of characteristic skull shapes occurs and the position of the eyes is often influenced. No systematic investigation of the interpupillary distance in defectives seems to have been undertaken hitherto. The present paper is intended as a contribution to the method of basing diagnosis upon exact measurement rather than on clinical impression.

## SUMMARY OF PREVIOUS LITERATURE

The interpupillary distance has been mainly studied in hypertelorism and mongolism. Barr ('04) noted the proximity of the eyes in mongolism and Brushfield ('24), on the basis of actual measurement, reached the same conclusion. Van der Scheer ('27) also noted that this distance is reduced in mongolism. Lowe ('49) found that the eyes of mongols were about 5 mm closer together than in normal adults though this fact had to be considered in relation to the small size of their heads and reduction of their measurements generally.

Kanner ('35), describing mongolism, states: "The eyes are very near each other, though the flat bridge of the nose may give the impression that they are spaced more widely." This impression has led many people astray; for example, Wilson ('40) says that the eyes are set obliquely and wide apart. Øster ('53) quotes observers, such as Weygandt, who also had stated that the distance was increased. Carter and McCarthy ('51) are not clear on this point and Engler ('49) was unable to find any divergence from the normal. Draper, Dupertuis and Caughey ('44) describe wide set eyes as a feature closely related to mongolism.

Greig ('24), for hypertelorism, observed that one of the most characteristic features was increased distance between the eyes.

## MATERIAL AND METHODS IN THE PRESENT STUDY

Patients measured for this survey were resident in Heckingham Institution, Little Plumstead Hall and Eaton Grange Hostel for Girls, Norfolk, or at Cell Barnes Hospital, Hertfordshire. Measurements of one mentally defective case of hypertelorism (at St. Lawrence's Hospital Caterham, Surrey) were kindly supplied by Dr. B. W. Richards. The writers are indebted to Dr. J. V. Morris and Dr. N. H. M. Burke for granting facilities for measuring the patients under their care.

The control group (for interpupillary distance) comprised 100 adult males and 100 adult females whose measurements were supplied by courtesy of Messrs. Clement Clarke of St. Albans: these measurements were taken for the purpose of fitting spectacles. One mentally normal case of hypertelorism, an adult male, was recorded in the data.

The measurement of the interpupillary distance was taken by the standard method. This consists in reading the distance, in millimeters, between the centers of the pupils on a transparent scale held at arm's length horizontally across the bridge of the subject's nose. The subject

is required to direct first one eye and then the other towards the opposite eye of the investigator. Thus readings are made as though the visual axes were parallel. Only those cases in which satisfactory cooperation could be obtained were used in this survey. If strabismus is present, the eye of the patient which is not being observed must be occluded.

In order to make a systematic analysis of the relationships between head size and interpupillary distance, and the changes involved with age, head length and head breadth were measured by standard anthropological methods for all patients in the survey. Head measurements of mentally normal controls were obtained from a sample of 192 male and 101 female adults, which included members of institution staffs, for comparison with an adult defective population.

The diagnoses and grades used in the tables (see also the key to tables 1 and 2), were checked by one of us (L. A. K.) who also measured all the defectives used in the survey.

### RESULTS

Since normal control measurements were available for these three measurements only in adult subjects, the main investigation covered 396 male and 302 female defectives aged 15 years and over. Even this grouping is not quite satisfactory since the head continues to grow after the age of 15 years. The results, by diagnosis and grade, are shown in tables 1 and 2. Measurements made on patients below the age of 15 years are summarized here and they show how all the measurements gradually increase with age. Unfortunately there are no normal controls available for comparison with them.

### KEY TO TABLES 1 AND 2

<i>Diagnosis</i>		
1 Mongolism	6 Endocrine	11 Epilepsy
2 Microcephaly	7 Hemiplegia	12 Psychosis
3 Acrocephaly	8 Diplegia	13 Miscellaneous (epi- loia, phenylketonuria, microphthalmos)
4 Hydrocephaly	9 Athetosis	14 Hypertelorism
5 Skeletal (other)	10 Neurological (other)	15 Residual group
<i>Grade</i>		
1 Idiot	2 Imbecile	3 Feeble-minded

TABLE I  
Head measurements of defectives and controls: males

Age	Diag- nosis	Grade	Interpupillary distance												No. of Cases	Mean measurements		I. d.÷ H. b.
			35- 39	40- 44	45- 49	50- 54	55- 59	60- 64	65- 69	70- 74								
			1	2	3	4	5	6	7	8	9	10	11	12				
0-4	All	4	6	0	1	2	4	1	2	.	.	.	10	47.5	131.0	158.5	0.36	
5-9	All	19	20	4	.	4	24	11	4	.	.	.	43	53.6	135.9	167.7	0.39	
10-14	All	13	30	6	.	.	10	27	12	.	.	.	49	57.0	141.0	174.6	0.40	
15+	1	0	17	0	.	1	8	7	1	.	.	.	17	54.6	142.6	172.3	0.38	
	2	2	2	0	.	.	1	1	3	.	.	.	4	60.0	123.2	173.2	0.49	
	3	2	2	0	.	.	1	1	1	2	.	.	4	62.8	149.5	183.2	0.42	
	4	3	1	0	.	.	2	1	1	.	.	.	4	55.5	159.5	198.2	0.35	
	5	0	7	0	.	.	1	1	6	.	.	.	7	61.7	144.9	186.3	0.43	
	6	3	4	3	.	.	2	2	2	3	1	.	10	60.4	142.0	184.5	0.42	
	7	1	9	3	.	.	5	5	3	5	.	.	13	62.4	141.2	183.5	0.44	
	8	9	10	2	.	.	.	5	13	2	1	.	21	61.5	139.1	181.0	0.44	
	9	0	4	2	.	.	.	1	3	2	.	.	6	62.8	147.0	188.7	0.43	
	10	5	22	15	.	.	2	10	22	7	1	.	42	61.4	145.0	188.8	0.42	
	11	7	14	18	.	1	7	19	19	9	3	.	39	62.3	147.3	189.6	0.42	
	12	7	18	18	.	.	1	6	24	11	1	.	43	62.3	147.7	186.5	0.42	
	13	2	3	1	.	1	.	2	4	.	.	.	6	59.8	142.8	180.3	0.42	
	14	0	1	0	.	.	.	.	.	1	.	.	1	67.0	148.0	178.0	0.45	
	15	9	57	113	.	.	7	50	98	23	1	.	179	60.7	145.4	185.7	0.42	
15+	All	50	171	175	.	1	24	98	200	65	8	.	396	61.0	145.0	185.5	0.42	
15+	Control measurements	.	.	.	.	.	.	7	54	31	8	.	100	64.3	151.5	194.6	0.42	
	S. D.	.	.	.	.	.	.	.	.	.	.	.	.	3.3	6.0	6.7	—	

\* I. d., interpupillary distance; the mean is based on ungrouped data.

† H. b., head breadth; H. l., head length.

TABLE 2  
Head measurements of defectives and controls: females

Age	Diagnosis	Grade		Interpupillary distance												No. of Cases	Mean measurements			I. d. ÷ H. b.	
		1	2	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	I. d.*	H. b.†	H. l.†	I. d. ÷ H. b.						
0-4	All	5	2	1		3	4					48.2	125.7	154.5	8	55.4	162.3	0.38			
5-9	All	6	10	1		4	6	0	1			53.3	133.2	158.5	17	55.0	167.0	0.40			
0-14	All	2	14	5		2	5	9	5			55.9	135.1	170.8	21	62.0	177.0	0.41			
15+	1	0	16	0			4	12							16	55.4	140.4	0.39			
	2	0	1	1			1	1							2	55.0	134.5	0.41			
	3	0	2	0				2							2	56.0	147.0	0.38			
	4	0	2	0					2						2	62.0	174.5	0.35			
	5	0	14	5			3	10	5	1					19	58.6	139.1	0.42			
	6	0	3	8				3	8						11	60.5	143.8	0.42			
	7	0	3	2				1	2	2					5	61.8	137.0	0.45			
	8	5	8	4			1	5	10	1					17	59.8	137.6	0.43			
	9	1	3	3				3	3	1					7	60.4	139.1	0.43			
	10	1	8	17				1	8	9	2				20	60.5	141.2	0.43			
	11	3	14	15					10	19	2	1			32	61.2	141.5	0.43			
	12	0	9	18				2	12	1					27	59.2	143.1	0.41			
	13	0	2	1					2		1				3	60.0	133.7	0.45			
	14	0	0	0											0	—	—	—			
	15	2	46	91			1	6	61	58	13				139	50.5	142.0	0.42			
15+	All	12	131	159		1	18	130	128	24	1	302	50.5	141.5	177.1			0.42			
15+	Control measurements						3	32	55	10		100	60.6	145.8	186.1			0.42			
	S. D.												3.0	5.4	7.0			—			

\* I. d., interpupillary distance; the mean is based on ungrouped data.

† H. b., head breadth; H. l., head length.



The three measurements can be investigated in any clinical group of adult defectives. Outstanding examples are mongolism, microcephaly, hydrocephaly, and hypertelorism. In all, 4 cases of hypertelorism were examined; they are males of whom three are defective and one is of normal mentality. The measurements are as follows:

Age	Grade	Interpupillary distance	Head breadth	Head length
9 <sup>1</sup>	idiot	63	127	163
15 <sup>1,2</sup>	imbecile	67	148	178
22 <sup>2</sup>	imbecile	78	158	202
49	normal	73	146	181

<sup>1</sup> See table 1.

<sup>2</sup> See table 3.

Three of these cases are adults and their mean interpupillary distance measurement is 72.7, almost  $2\frac{1}{2}$  times S. D. (standard deviation) above the control mean of 64.3. Since adult Africans in Jamaica have a mean measurement of 70.6 (Davenport and Steggerda, '30) it is clear that hypertelorism is not necessarily an abnormal trait but is usually a variation on a graded scale. The value of 78, in the third case recorded above, must, however, be regarded as grossly abnormal for a European.

When all measurements are expressed in terms of standard deviations exact comparisons can be made, and the difference divided by the standard deviation is given in table 3 for the three measurements in the various outstanding types.

It is clear that in the mongols the length of the head is greatly diminished,  $-3\frac{1}{2}$  S. D., and that the head breadth is only slightly less than the normal control; interpupillary distance is markedly, about  $-2$  S. D., different from the normal. In the case of microcephaly, head length is diminished less than that of the mongols, head breadth is more diminished than that of the mongols; the interpupillary distance is small in these cases, as might be expected, but, in relation to head breadth, it is not diminished as it is in mongolism.

Hydrocephaly is associated with increased head length and, especially, breadth of the head but the interpupillary distance is not increased and may even sometimes be markedly diminished.

The interrelationships between these three head measurements are of biometric interest. In order to study them precisely, correlation coefficients were calculated on the total data, pooling all patients of different

TABLE 3

*Analysis of head measurements by clinical type (age 15 years and over)*

Diagnosis	Number	Sex	Measurement	Mean	Difference from Control* (D)	(D) ÷ (S. D.)*
1 Mongolism	17	m	Interpup. dist.	64.3	— 0.7	—2.9
			Head breadth	142.6	— 8.9	—1.5
			Head length	172.3	—22.3	—3.3
	16	f	Interpup. dist.	55.4	— 5.2	—1.7
			Head breadth	140.4	— 5.4	—1.0
			Head length	162.3	—23.8	—3.4
	33	m & f †	Interpup. dist.			—2.3
			Head breadth			—1.3
			Head length			—3.3
2 Microcephaly	4	m	Interpup. dist.	60.0	— 4.3	—1.3
			Head breadth	123.2	—28.3	—4.7
			Head length	173.2	—21.4	—3.2
	2	f	Interpup. dist.	55.0	— 5.6	—1.3
			Head breadth	134.5	—11.3	—2.1
			Head length	167.3	—19.1	—2.7
	6	m & f †	Interpup. dist.			—1.5
			Head breadth			—3.8
			Head length			—3.0
4 Hydrocephaly	4	m	Interpup. dist.	55.5	— 8.8	—2.7
			Head breadth	159.5	+ 8.0	+1.3
			Head length	198.2	+ 3.6	+0.5
	2	f	Interpup. dist.	62.0	+ 1.4	+0.5
			Head breadth	174.5	+28.7	+5.3
			Head length	202.0	+15.9	+2.3
	6	m & f †	Interpup. dist.			—1.6
			Head breadth			+2.6
			Head length			+1.1
14 Hypertelorism	3	m	Interpup. dist.	72.7	+ 8.4	+2.5
			Head breadth	150.3	— 1.2	—0.2
			Head length	187.0	— 7.6	—1.1

\* See tables 1 and 2.

† Weighted mean.

ages (see table 4). Naturally, there were positive correlations between age and each measurement and these had to be eliminated statistically. The degrees of association of the measurements for constant age were found by applying partial correlation technique. Interpupillary distance was shown to be closely related to head length. It was therefore concluded that, for clinical purposes, comparison of interpupillary distance with head breadth, rather than with length, would give the most useful information.

TABLE 4  
*Correlation coefficients*

Characters	Males (498 cases)	Females (348 cases)
Interpupillary distance and head breadth	$+0.493 \pm 0.034$	$+0.450 \pm 0.043$
"          "          and head length	$+0.660 \pm 0.025$	$+0.598 \pm 0.034$
"          "          and age	$+0.440 \pm 0.036$	$+0.351 \pm 0.047$
Head breadth and head length	$+0.570 \pm 0.030$	$+0.493 \pm 0.041$
"          "          age	$+0.204 \pm 0.043$	$+0.219 \pm 0.051$
Head length and age	$+0.380 \pm 0.038$	$+0.355 \pm 0.047$
Interpupillary distance and head breadth, for constant age	$+0.459$	$+0.408$
Interpupillary distance and head length, for constant age	$+0.593$	$+0.541$

A simple way of indicating the peculiarities observed, on the one hand in mongolism and, on the other, in hypertelorism, is to examine the index (interpupillary distance  $\div$  head breadth). This index has some advantage over the traditional one, obtained by dividing interpupillary distance by face breadth. The head breadth is available and known to be useful for clinical purposes whereas face breadth is not.

The index, interpupillary distance divided by head breadth, was found to vary between 0.30 and 0.51. There are no controls available directly for this index but the average value for normal European adults must be close to 0.42. The mean values of I. d. and H. b. ( $m_a$  and  $m_b$  respectively) for controls, given in tables 1 and 2, their S. D. values ( $s_a$  and  $s_b$  respectively) and the intercorrelation between these two measurements corrected for age ( $r_{ab}$ ) can be used to estimate the normal value of the index ( $a/b$ ) and its standard deviation ( $s_{a/b}$ ). Thus,

$$(s_{a/b})^2 = (m_b^2 s_a^2 - 2m_a m_b s_a s_b + m_a^2 s_b^2) / b^4$$

Assuming that  $m_{a/b} = m_a/m_b$ , the index for control males has a mean of 0.420 with S. D. of 0.021 and the mean index for control females is 0.416 with S. D. of 0.020. Distributions derived from defectives and controls are summarized in table 5 and figure 1 has been constructed from table 6.

TABLE 5

*Mean interpupillary distance ratio (distance/head-breadth)  
in different sample populations*

Description of cases	Age Group in years	Number	Mean Ratio	Standard Deviation
Mongolism	0 to 14	30	0.385	0.019
	15 & over	33	0.390	0.021
Hypertelorism	all ages	3	0.480	0.026
Other types of defectives	0 to 14	117	0.402	0.031
	15 & over	604	0.423	0.029
Control males	15 & over	100	0.420	0.021
Control females	15 & over	100	0.416	0.020

TABLE 6

*Percentage distribution of interpupillary ratio in defectives*

(a/b) * Ratio	Cases of Mongolism	Cases of Hypertelorism	All Other Cases
0.50+		33.3	0.9
0.47-0.49	0.0	33.3	5.4
0.44-0.46	0.0	33.3	24.3
0.41-0.43	0.0	0.0	39.6
0.38-0.40	14.3	0.0	23.7
0.35-0.37	61.9	0.0	5.2
0.32-0.34	20.6	0.0	0.8
-0.31	3.2	0.0	0.1
	0.0		
Total	100.0	99.9	100.0
Number of cases	63	3	781

\* Interpupillary distance  $\div$  head breadth.

The average of this index, for all defectives, agrees with the control: it is slightly less than this in infants (see tables 1 and 2).

In mongols the average is between 0.38 and 0.39. As in many other characters the mongols show less variation than other defectives here. The standard deviation is just 0.02, instead of nearly 0.03 in the other cases. The index is also notably low in hydrocephaly.

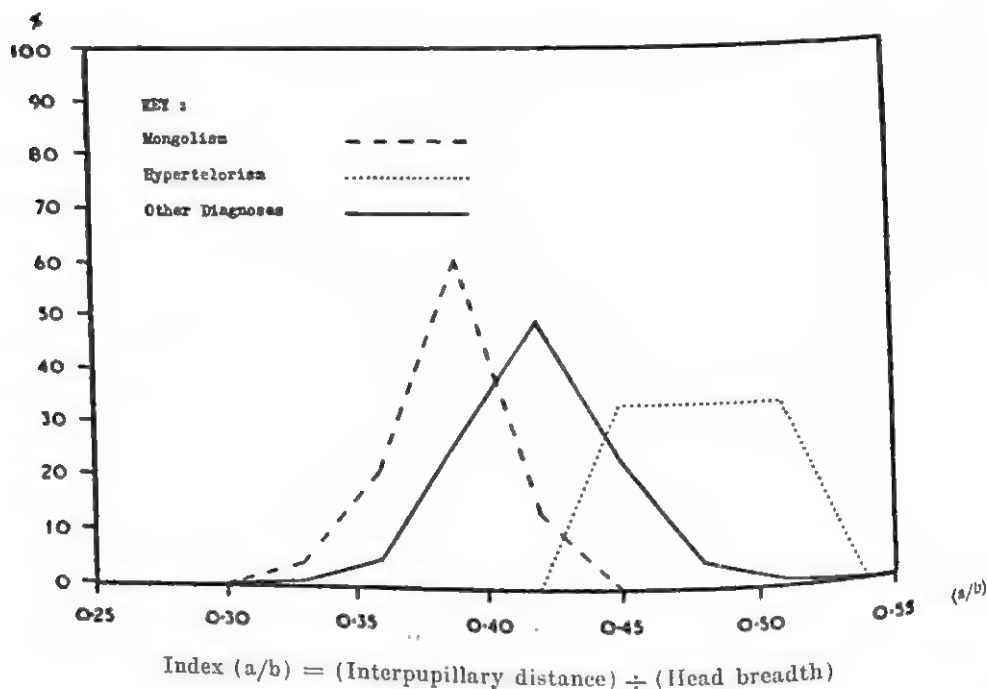


FIG. 1. PERCENTAGE DISTRIBUTIONS OF MENTALLY DEFECTIVE PATIENTS (ALL AGES).

#### SUMMARY

Interpupillary distance has been measured in 498 male and 348 female defectives and related to head breadth and head length. Comparisons were made between the measurements of adult defective and normal adult controls.

It is found that the ratio of interpupillary distance to head breadth is a useful clinical index. This ratio, which has a normal value of 0.42, with a standard deviation of 0.02, is much greater in hypertelorism (0.48) and much less in mongolism (0.38).



## LITERATURE CITED

- BARR, W. M. 1904 Mental Defectives, their History, Treatment and Training. Rebman Ltd., London.
- BRUSHFIELD, T. 1924 Mongolism. *Brit. J. Child. Dis.*, Lond., 21:241-258.
- CARTER, C. O. AND D. MCCARTHY 1951 Incidence of mongolism and its diagnosis in the newborn. *Brit. J. Soc. Med.*, 5: 83.
- DAVENPORT, C. B. AND M. STEGGERDA 1930 Race Crossing in Jamaica. Carnegie Institute Publication, Washington.
- DRAPER, G., C. W. DUPERTUIS AND J. L. CAUGHEY 1944 Human Constitution in Clinical Medicine. Paul B. Hoeber, New York.
- ENGLER, M. 1949 Mongolism (Peristatic Amentia). Simpkin Marshall, Ltd., London.
- GREIG, D. M. 1924 Hypertelorism: a hitherto undifferentiated congenital cranio-facial deformity. *Edinb. Med. J.*, n. s. 31: 560-593.
- KANNER, L. 1935 Child Psychiatry. Charles C. Thomas, Springfield.
- LOWE, R. M. 1949 The eyes in mongolism. *Brit. J. Ophthalmol.*, 33: 131-174.
- ØSTER, J. 1953 Mongolism. Ejnar Munksgaard, Copenhagen.
- VAN DER SCHEER, W. M. 1927 Beiträge zur Kenntnis der mongoloiden Missbildung. *Abh. Neurol. Psychiat. Psychol.*, 41: 1-162.
- WILSON, S. A. K. 1940 Neurology, Vol. 2. Edward Arnold and Co., London.





## THE ABO, MNS, AND Rh-Hr BLOOD GROUPS OF THE MAPUCHE INDIANS OF CAUTÍN PROVINCE, CHILE

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### INTRODUCTION

THE purpose of this paper is to present fuller serological data on the Mapuche Indians, align these data with previously published figures on the Mapuche (Rahm, '31; Henckel, Castelli and Dal Borgo, '41; and Sandoval, Henckel and Givovich, '46), and to discuss the hypothetical gene frequencies of pure blood Mapuche in view of the amount of White admixture in these series. The present series was collected by us in December, 1953, with the encouragement of and a grant from the Council of Scientific Investigations of the Universidad de Concepción. After establishing a field laboratory at the Hospital Regional de Temuco, we were able to secure blood samples from 266 Mapuche located in Temuco and five towns within the province (see table 1). Because of poor samples or obvious White admixture, 8 were not used. Through Drs. A. E. Mourant and R. R. Race we were able to secure a small amount of anti-S serum. Anti-Rh<sub>0</sub>(D), anti-rh'(C), anti-rh''(E), anti-Hr'(c), and the anti-M and anti-N sera were purchased from the Blood Donor Service, Jamaica, New York. Anti-sera for the ABO groupings were prepared by Dr. Sandoval from the Blood Bank Service, St. Borja Hospital, Santiago.

### MATERIAL AND RESULTS

A full examination was made of the A<sub>1</sub>A<sub>2</sub>BO, and Rh groups of the main series of specimens. The frequencies of the ABO groups are shown in table 2. In calculating the gene frequencies, the Bernstein's formulae, adjusted, were used.

As we expected, the higher frequency of group O and of gene O were in good agreement with our earlier investigations in the same province. Duplication of our previous results in respect to frequencies of the ABO

TABLE 1

Locality	Total	Not tabulated
Temuco (Prison)	10	
Temuco ("Tucapel" Regiment)	25	
Temuco (Hospital)	18	No. 192 Poor sample. No. 209, White.
Cajon (Sanitary Unity)	12	
Cajon (Public School)	15	
Cajon (Farmer School)	20	
El Natre (School)	24	No. 108 Poor sample.
Arquenco (Public School)	16	
Arquenco (House)	5	
Labranza (Unicef)	12	No. 142 "mestizo." No. 143 Poor sample.
Labranza (Public School)	44	No. 148 (Borona type, Blue eyes) No. 279, Red hair.
Cholchol (Huichican School)	57	
Total tabulated	258	

TABLE 2

*The ABO system*

	Total	O	Group			Gene Frequencies		
			A <sub>1</sub>	B	AB	A	B	O
Number	258	205	35	18	0	0.0701	0.356	0.8939
Per cent	99.98	79.45	13.56	6.97	0			

Calculated by Bernstein's formulae.

groups suggests that there has been no important change in the genetic nature of the population during the 8 years which intervened.

The frequencies of the Rh-Hr groups are shown in table 5. The gene frequencies were calculated from Fisher's formulae (see Race and Sanger, '50). All the Mapuche Indians were Rh positives.

The  $R_1$  (CDe) gene frequency was also significantly higher than gene  $R_2$  (cDE) frequency. Genes  $r$  (cde);  $r'$  (Cde); and  $r''$  (cdE) were lacking in our series.

MNS frequencies (see table 3) have not been reported previously from Chile. Our findings on a small sample (59 individuals) are comparable to Chown's data on the Blood Indians of Canada (see Chown

TABLE 3  
*The MNS system*

	Total	MS	NS	MNS	Ms	Ns	MNs
Number	59	17	4	17	13	1	7
Per cent	99.99	28.81	6.78	28.81	22.03	1.70	11.86

Gene Frequencies

mS	.2438
ms	.4686
nS	.1288
ns	.1596

Calculated by Mourant's formulae.

and Lewis, '53). These frequencies are distinctly higher than Salazar-Mallen's ('52) on the Tarasco and Otomí of Mexico; the figures obtained by Sanger ('50) on Australian and New Guinea natives; those from Zotendick ('53) on Bushmen; and those published by Pantin ('53) on Diegueño Indians.

The MN frequencies calculated from Wiener's formulae, alone, in a larger sample (144 individuals) were in good agreement with our earlier figures (see table 4).

TABLE 4  
*The MN system*

	Total	M	Group		Gene Frequencies	
			N	MN	m	n
Number	144	68	12	64		
Per cent	99.99	47.22	8.33	44.44	0.6944	0.3055

Calculated by Wiener's formulae.

## DISCUSSION

The history of Araucanian (Mapuche)-White contact in Chile dates from 1541 (see Cooper, '50) and is of such nature as to virtually preclude the selection of a completely "pure" Indian series among the Mapuche. Since, according to the 1920 census, 58,000 of the 105,000 Mapuche were then located in Cautín province, it is apparent that there lay the best opportunity of securing the relatively purest Indian samples. This

TABLE 5  
*The Rh-Irr system*

	Total	Rh <sub>1</sub> Rh <sub>1</sub> CCDe	Rh <sub>1</sub> rh CcDe	Rh <sub>1</sub> Rh <sub>2</sub> CcDE	Rh <sub>2</sub> ccDE	Rh <sub>0</sub> cDe	Rh <sub>2</sub> Rh? CCDE
Number	258	113	21	77	32	11	4
Per cent	99.97	43.79	8.13	29.84	12.4	4.26	1.55

Gene frequencies			
R <sub>0</sub> (cDe)	0.021	r (cde)	0.000
R <sub>1</sub> (CDe)	0.693	r' (Cde)	0.000
R <sub>2</sub> (cDE)	0.255	r''(cdE)	0.000
R <sub>4</sub> (CDE)	0.032		

Calculated from Fisher's formulae.

opportunity, of course is, what brought us to Cautín province. However, despite all the care we could exercise, it is likely that the series has White admixture.

If we had any clear idea of the genetic composition of the Indian and the White populations, the blood group frequencies of our Mapuche series could be used in estimating the amount of intermixture. Failing precise data on the parent populations, we have the agreement of Boyd ('49, p. 591) that such estimates are probably not worthwhile. It is also worth noting that even with much better information than we have on the gene frequencies of the parent populations, Chown and Lewis ('53, p. 380) are only willing to estimate that roughly one-sixth of the genes in their Blackfoot and Blood Indians series are attributable to Whites.



It is likely that White admixture in our Mapuche series is greater than the one-sixth for Blackfoot and Blood. Indeed, by employing various formulae on the ABO and MN frequencies, estimates of White admixture range from 30-47%. Unfortunately, these estimates are only based upon hypothetical or assumed frequencies for the White and Indian populations of Chile. For example, using Steven's ('52, pp. 17-20) formulae for  $p$  and  $q$ , we may assume parent White frequencies of 0.27 and 0.08 respectively, and none for either in the case of the pre-contact Mapuche. Yet since all the Mapuche A fell in subgroup  $A_1$ , with no  $A_2$  such as occurs in roughly one out of 4 or 5 group A Europeans, it is by no means certain that the pre-contact Mapuche had no group A. In any case, Stevens' formulae yield an estimated 30% White admixture.

Done another way, by using the simple Ottensooser's ('44) formula on group B, alone, we may assume a frequency of 0.08 for the Whites and none for the pre-contact Mapuche. While it is most likely that the group B now shown by the Mapuche had a White origin, the assumption of 0.08 for  $q$  in the Whites may not be close to reality. The estimated amount of White admixture by this overly simplified formula is about 44%. Finally, another estimate may be sought in the MN groups, using the simple formula cited by Boyd ('49, pp. 587-588). Here we have assumed that the White frequency for  $n$  would be about 0.42, and since American Indians are high in M and low in N, that a pre-contact Mapuche  $n$  frequency would be about 0.20. This estimate of White admixture runs about 47%.

It seems to us, however, that these estimates are altogether too high, specially when  $r$ ,  $r'$  and  $r''$  (cde, Cde, and cdE) are wholly lacking in the present Mapuche series, although there was a low incidence of these factors in a previously reported one (Sandoval, Henckel, and Givovich, '46). Some incidence of these genotypes could be expected in a population with considerable White admixture; for instance, in a series of 241 Blood Indians gene  $r$  had a frequency of 0.06 (Chown and Lewis, '53).

In summary, with no more information than is available to us at present, we cannot give any confident estimate of the amount of White admixture in the Mapuche series. Without any more than the above considerations and our own experience to guide us, we suggest that the White admixture may be somewhere around 25%.

For the translation into English, revision of our work, and numerous kind suggestions we should like to thank Dr. Richard P. Schaedel and Dr. Marshall T. Newman.

## SUMMARY

The ABO, MNS and Rh blood groups of 266 Mapuche Indians located in Cautín province have been examined, and 258 anthropologically selected individuals have been studied. High frequency of the O characteristic of the American Indian series was found. Of the A group, only subgroup  $A_1$  was present. There was no  $A_2$ .

M was high. S was higher than in other series investigated in Central America. All the Mapuche Indians were Rh positive. The genes  $r$  (ede);  $r'$  (Cde); and  $r''$  (edE) were absent from the series.

The appraisal of White admixture is discussed, and reasons are given for supposing this admixture to be around 25%.

## LITERATURE CITED

- BOYD, W. C. 1949 Gene frequencies and race mixture. *Am. J. Phys. Anthropol.*, n. s. 4: 587-593.
- CHOWN, B., AND M. LEWIS 1953 The ABO, MNSs, P, Rh, Lutheran, K, Lewis, Duffy and Kidd blood groups and the secretor status of the Blackfoot Indians of Alberta, Canada. *Am. J. Phys. Anthropol.*, n. s. 11: 369-384.
- COOPER, J. M. 1950 The Araucanians. *Handbook of South American Indians*, 2: 687-700.
- HENCKEL, C., CASTELLI, AND DAL BORGO 1941 Algunas observaciones acerca de los grupos sanguíneos M y N en los Indios Mapuche. *Boletín Soc. Biología de Concepción (Chile)* 15: 37-41.
- OTTENSOOSER, F. 1944 Cálculo do grau de mistura racial a través do grupo sanguíneo. *Rev. Bras. Biol.* 4: 531-537. "
- PANTIN, A. M., AND R. KALLSEN 1953 Blood groups of Diegueño Indians. *Am. J. Phys. Anthropol.*, n. s. 11: 91-96.
- RAHM, G. 1931 Sobre los grupos sanguíneos de los Fueguinos. *Bol. Soc. Biología de Concepción (Chile)*, 6-7: 59-61.
- SALAZAR-MALLEN, M., *et al.* 1952 Blood agglutinogens of the Mexicans. *Annals of Eugenics*, 16: 351-358.
- SANDOVAL, L., C. HENCKEL AND L. GIVOVICH 1946 The blood groups, subgroups and Rh Factor of the Mapuche Indians of the Province of Cautín (Chile). *Blood*, 1: 555-559.
- SANGER, R. 1950 The MNS blood groups of the Australian aborigenes and New Guinea natives. *Nature*, 165: 939-942.
- STEVENS, W. L. 1952 Statistical analysis by the ABO system in mixed populations. *Human Biol.*, 24: 12-24.
- WIENER, A. S., *et al.* 1945 Individual blood differences in Mexican Indians with special reference to the Rh blood types and Hr factor. *J. Exp. Med.*, 81: 559-571.
- ZOUTENDIK, A. M., AND A. KOPEO 1953 Blood groups of Bushmen. *Am. J. Phys. Anthropol.*, n. s., 11: 361-368.



## FURTHER EVIDENCE OF AGE CHANGES IN BODY FORM BASED ON MATERIAL OF D. A. W. EDWARDS

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TO get more evidence on the age changes in the main patterns of body form, the data collected in London by Edwards ('51) and presented in his table III are reevaluated. It may be said at the outset that results are similar to those on Minnesota women (Škerlj, Brožek and Hunt, '53). Howells ('52), for males, and Škerlj ('30 and '38), for females, have also approached this problem with studies of other series.

The questions to be investigated are:

1. Whether Edwards' data, arrived at by measuring the thickness of a fold of skin and subcutaneous fat (skin fold) at 53 sites, support the results obtained by measuring at 10 sites, in women, or even fewer sites, in men (cf. Škerlj, Brožek, and Hunt, '53).
2. Whether there is really no difference between nulliparous and parous women, as claimed by Edwards; and
3. Whether there are differences with sex and age in certain parts of the body; that is, whether there are differences in the degree of development of the superficial soft tissues in the superior as against the inferior part of the body or in the trunk as compared with the limbs (cf. Škerlj, '30 and '38 and Škerlj *et al.*, '53).

Edwards ('51, pp. 305-306) measured with a skinfold caliper. He says:

The observations were on patients in the Medical Outpatient Department, in wards, and in the Endocrine Clinic of the Obstetric Hospital. The patients were at first taken at random as they came to the hospital but were later selected according to their total amount of subcutaneous fat, to provide an even distribution of patients over a wide range of obesity in each of the groups described below. Patients were excluded from the series if they suffered from lipodystrophy, oedema, any wasting disease, or any proved endocrine disorder. They were not excluded because of menopausal irregularities only.

The patients were arranged according to sex and maturity in the following groups: 18 prepubertal boys—males of 5 years or older without pubic hair; 10 pubertal boys—males with pubic hair who were not more than 15 years old; 16 men—males of 19 years and older; 14 prepubertal girls—females of 5 years or older whose menarche had not occurred; 22 pubertal girls—females whose menarche had occurred not more than 5 years previously; and, of women whose menarche had occurred at least 5 years previously, 72 nulliparous—who had never been pregnant, 55 parous—but who had not been pregnant within the past year; and 26 menopausal who had had signs or symptoms of menopause regardless of whether they had ever been pregnant or not. Ten additional women who were pregnant at the time of measurement are not further considered here.

In all these individuals skin folds were measured at 53 sites: one on the chin, two on the neck, 10 on the front and side of the thorax, three on the abdomen, 9 on the back and lumbar region, 8 on the upper arm, 8 on the forearm, and 6 each on the thigh and calf.

Following Edwards (51) the skinfold thicknesses are expressed in percentages of the sum of all 53 measurements. As the numbers in some groups are small some irregularities due to the effects of sampling must be expected.

In the neck, thorax, abdomen, the front and the back, the increase of relative skinfold thickness in males, particularly between puberty and adulthood, is more intensive than it is in females.

There are two peculiarities in these regions in females: 1. the relative fat thickness decreases from prepuberty to puberty in the neck, abdomen and the total front; it decreases from prepuberty to the nulliparous state in the front of the thorax; but it increases from the prepubertal age-group on in the back of the thorax and the total back; 2. the parous women show, in all these regions, except the abdomen, a reversion toward the prepubertal or pubertal state or, at least, the parous women are not intermediate between the nulliparous and menopausal adult females; at any rate, there are at least slight differences between the parous and non-parous.

The lumbar region shows no big differences in the main trend, even though here also males gain more between puberty and adulthood than between prepuberty and puberty. The parous women again reverse the female trend and resemble the pubertal girls; taking the back as a whole, this reversion toward the pubertal condition is very impressive.

In the upper arm, males show almost no differences. The females, however, lose relatively from the prepubertal to the pubertal state, gain to the parous state and then lose again. The total increase in the upper arm is, therefore, very small in females also. In the forearm in both sexes the relative skinfold thickness decreases almost equally except that, in females, the parous women gain a little and the menopausal ones rank below them but above pubertal and nulliparous females.

Considering the trunk above the waist, the relative skinfold thickness increases very intensively in males but much less in females, among whom there is a reversal in the parous state toward pubertal and prepubertal levels. In the trunk below the waist there is also an increase in both sexes; in females the pubertal ones rank lowest and thereafter there is an increase at each stage, although not much in the parous group. When the whole trunk is considered the differences appear even more strikingly: the males gain very intensively, whereas in the females the tendency to increase is broken by the pubertal girls being below the prepubertal ones and parous ones being below the nulliparous; even the menopausal women are far below the adult men in this respect and the parous and nulliparous women are even below the pubertal boys.

In the limbs there is a tendency for the relative skinfold thickness to decrease, particularly in the legs. Pubertal girls show a decrease in the upper limbs but later there is a slight increase. Just the opposite is true of the lower limb: the skin folds are thickest in the pubertal girls, the nulliparous women show a decrease nearly to the prepubertal level, and the parous and especially menopausal women have relatively still smaller skinfold measurements of the inferior extremity. The adult males show an even greater decrease.

There is an interesting sex difference in the distribution of subcutaneous fat in the limbs. In the upper arm of females there seems to be a tendency to lose subcutaneous fat with age at the sites where it is thickest. This is not the case with males, even though there is such a tendency for fat on the inner aspect. In the arm of both sexes the thickest skinfold is proximal, the thinnest one distal except in pubescent boys, in whom the minimum is on the medial side near the arm pit. In the forearm the maxima are proximal in all groups and the minima distal, but there are variations in whether these are anterior, posterior, medial or lateral (*cf.* Edwards, '51, table III).

In the thigh in both sexes the maxima are proximal and the minima



distal, though again there are variations in the exact location of these.

In the calf the greatest skinfold thickness in females is found on the median aspect just under the knee, and the minima are regularly on the lateral aspect above the ankle. The males are the same as the females except that in prepubescent boys the maxima is on the medial side just above the ankle and the minima is just below the knee.

Considering both extremities, the general tendency in both sexes is to lose subcutaneous fat, particularly from the distal parts.

In the comparison of prepubescent children and the most mature group, it is interesting that, in all respects except the upper arm, the differences are far greater in males than in females. This seems to suggest that males change in body form with age more than do females. The increase in skinfold thickness on the neck and trunk, as well as the decrease on the limbs, is more intensive in men. This is particularly true of the skinfold over the upper part of the spines as well as over the abdomen, on the one hand, and over the thigh and calf, on the other. One is challenged to connect these great changes in the distribution of soft tissues in males with a life expectancy which (in the experience of life insurance companies everywhere) is below that of females. At present this question is perhaps too speculative, but it may be asked whether there is a connection with cholesterol in blood and with atherosclerosis.

In conclusion, then, this analysis, first, supports and enlarges on our previous statement and guess (Škerlj, *et al.*, '53), namely that there is an overall trend with age to lose subcutaneous fat in the limbs, particularly in their distal parts (at least relative to other skinfold thicknesses). We have shown, furthermore, that this trend can be observed in only 10 (or, in men, even fewer) measurements on each person. This is encouraging, for there is seldom time enough on a sufficient number of volunteers for measuring 53 sites or even more (*cf.* Pochin, cited by Edwards, '50), not to mention practical considerations in clinical work when time is an even more important factor.

Second, in respect to the relative skinfold thicknesses, at least in some parts of the body, it seems that the parous women resemble the prepubescent and pubescent girls more than do the nulliparous and menopausal women. This statement does not support the one expressed by Edwards, and further investigation of this question would be useful. At any rate, from tables 1 and 2 it can be seen immediately that many of the percentages for parous women show a tendency to return towards

TABLE 1

Average skin-fold thicknesses as percentages of total for 53 sites \*

Group	Females					Males			
	Pre-pubescent	Pubescent	Nulliparous	Parous	Menopausal	Pre-pubescent	Pubescent	Mature	
Number	14	22	72	55	26	18	10	16	
Total skin-fold thicknesses in mm	982	977	1530	896	1001	733	852	662	
Neck	3.4	3.1	3.3	3.4	3.5	3.6	3.6	4.4	
Thorax front	15.1	14.7	14.5	14.5	16.1	15.7	16.8	18.4	
Thorax back	11.6	12.1	13.3	13.0	13.6	10.8	11.4	15.5	
Abdomen	8.5	7.6	7.9	8.4	9.2	8.1	8.5	10.3	
Lumbar region	3.4	3.9	4.2	3.9	4.2	3.2	3.5	4.8	
Upper arm	15.5	15.1	15.8	16.2	15.9	14.6	14.7	14.6	
Forearm	9.6	7.8	7.6	7.9	7.8	9.8	8.3	7.2	
Thigh	20.6	22.9	21.4	20.8	18.9	20.4	20.2	15.6	
Calf	12.3	12.9	12.0	12.0	10.5	13.9	13.1	9.3	

\* The sites are illustrated in Edwards (51, Fig. 1A). Neck: A<sub>1,2</sub>; E<sub>1</sub>. Thorax front: A<sub>3,4</sub>; B<sub>1,2,3,4</sub>; C<sub>1,2,3,4</sub>. Back: D<sub>1,2,3,4</sub>; F<sub>2,3,4</sub>. Abdomen: A<sub>5,6</sub>; B<sub>5</sub>. Lumbar region: D<sub>5</sub>; F<sub>5</sub>. Upper arm: AF<sub>1,2</sub>; AB<sub>1,2</sub>; AO<sub>1,2</sub>; AI<sub>1,2</sub>. Forearm AF<sub>3,4</sub>; AB<sub>3,4</sub>; AO<sub>3,4</sub>; AI<sub>3,4</sub>. Thigh: LF<sub>1,2</sub>; LB<sub>1,2</sub>; LO<sub>1,2</sub>. Calf: LB<sub>3,4</sub>; LO<sub>3,4</sub>; LI<sub>1,2</sub>.

TABLE 2

*Relative skin-fold thicknesses as percentages of total on the main parts of the body \**

Group	Females				Males			
	Pre-pubescent	Pubescent	Nulliparous	Menopausal	Pre-pubescent	Pubescent	Mature	
Neck	3.4	3.1	3.3	3.5	3.6	3.6	4.4	
Trunk above the waist	26.6	26.8	27.8	29.8	26.5	28.2	33.9	
Trunk below the waist	11.9	11.5	12.1	13.3	11.3	12.1	15.1	
Upper limb	25.2	22.9	23.3	23.7	24.4	23.0	21.8	
Lower limb	32.9	35.8	33.5	29.4	34.3	33.4	24.8	
<i>S</i> vector	30.0	29.9	31.1	33.3	30.1	31.8	38.3	
<i>I</i> vector	70.0	70.1	68.9	66.5	70.0	68.4	61.7	
<i>Tr</i> vector	41.0	41.3	43.2	46.6	41.4	43.8	53.4	
<i>Ex</i> vector	58.1	58.7	56.8	53.2	58.7	56.3	46.7	

\* Trunk above the waist: thorax, front and back. Trunk below the waist: abdomen and lumbar region. Upper limb: arm and forearm. Lower limb: thigh and calf. *S* vector: neck and trunk above waist. *I* vector: trunk below the waist and limbs. *Tr* vector: trunk and neck. *Ex* vector: limbs.

those of the younger groups, the prepubescent girls in particular. Even though one tries to think imaginatively about the question, why parous women resemble prepubertal and pubertal girls more than do nulliparous women, an answer, at present, would be more speculative than plausible. And frankly, I, for one, can not as yet find even a reasonable speculative answer.

As to our third question, the changes in relative skinfold thicknesses between the least and most mature groups are greater in the males than in the females. In the neck the increase is about 8 times as great in males as in females. In the trunk above the waist the gain in men is more than twice that in women, and in the trunk below the waist it is almost three times greater. In the total trunk the gain in males is therefore almost three times that in females. Furthermore, the relative loss of fat on the extremities, particularly the lower one, is far greater in men.

In table 2 it may be seen that the skinfolds of the superior part of the body (*S* vector) increase while those of the inferior part (*I* vector) decrease with age. This trend occurs in both sexes but is more marked in males. Similarly there is an increase in skinfolds of the trunk with age (*Tr* vector) as compared to the extremities (*Ex* vector), and this is an even more apparent contrast, particularly in the males. In both these vector continua, the status of the parous females barely break the main tendency to steady change with increased maturity. These results fully support those of Škerlj, Brožek and Hunt ('53) on Minnesota women.

### LITERATURE CITED

- EDWARDS, D. A. W. 1950 Observations on the distribution of subcutaneous fat. *Clin. Science*, 9: 259-270.
- EDWARDS, D. A. W. 1951 Differences in the distribution of subcutaneous fat with sex and maturity. *Clin. Science*, 10: 305-315.
- HOWELLS, W. W. 1952 A factorial study of constitutional type. *Amer. J. Phys. Anthropol.*, n. s. 10: 91-118.
- ŠKERLJ, B. 1930 Zur physiologischen "Fettleibigkeit" des Weibes. *Arch. Frauenkunde*, 16: 235-246.
- ŠKERLJ, B. 1938 Die Körperformtypen des Weibes. *Acta Neerl. Morph. Norm. et Pathol.*, 2: 20-41.
- ŠKERLJ, B., J. BROZEK, AND E. E. HUNT, JR. 1953 Subcutaneous fat and age changes in body build and body form in women. *Amer. J. Phys. Anthropol.* n. s. 11: 577-600.



## PHYSIQUE, TEMPERAMENT AND SEX RATIO

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**D**URING a study of the relation of pulse rates of college students of 10-15 years ago to various personal and social factors, it was observed that men having the slowest pulses had more daughters than sons when they later married and had families, whereas men with the fastest pulses had more sons than daughters. When the whole range of pulse rates was considered, a relationship with sex ratio was not convincing. Pulse rate, however, is related to various factors of physique and temperament: very athletic men, for example, tend to have quite slow pulse rates. For this reason it was decided to compare at least some of the available factors of physique and temperament with the sex ratio of offspring.

The subjects selected for the Grant Study in 1938-1942 were college sophomores having good health and overtly good social adjustments (Heath *et al.*, '46). They have been followed to date, 191 of them having married and had children. C. C. Seltzer in 1938-1942 carefully somatotyped the young men. E. B. McTernan (Seltzer *et al.*, '48) "psychotyped" the men from their original psychiatric, social and medical records before 1947, when very few offspring had been born. Tables 1 and 2 show that the men in college who had been judged predominantly mesomorphic (the muscular, heavy boned) and predominantly somatonic (active, physical type of temperament), tended later to have an excess of daughters. Their opposites, the ectomorphic (the thin) and the cerebrotonic (intellectual temperament) tended to have an excess of sons (table 6).

\* The author wishes to thank Edward E. Hunt, Jr., Charles C. McArthur and Hugo Muench for their advice concerning this paper.



TABLE 1

*Predominant mesomorphy and sex ratio of offspring*

ALL CHILDREN			
	Males	Females	
Mesomorphy predominant	106	128	Total No. Families = 187
" not predominant	106	91	
Total	212	219	p = .08
FIRST-BORN			
Mesomorphy predominant	44	56	
" not predominant	50	37	
Total	94	93	p = .07

TABLE 2

*Predominant somatotonia and sex ratio of offspring*

ALL CHILDREN			
	Males	Females	
Somatotonia predominant	58	76	Total No. Families = 186
" not predominant	155	138	
Total	213	214	p = .07
FIRST-BORN			
Somatotonia predominant	21	35	
" not predominant	72	58	
Total	93	93	p = .03

There is a loose relationship between groups of college men classified by such criteria of physique and personality and their choices of major studies in college. Table 3 shows that those who had majored in the natural sciences tended to have offspring with a lower sex ratio than those who had majored in verbal, ideational or artistic subjects. The differences are consistent with the expected trends but cannot be considered significant.

In order to check whether the Grant Study findings might be due to an accident of sampling, the college class graduating in 1943 was

TABLE 3

*College field of concentration (major) and sex ratio of offspring*

ALL CHILDREN		
	Males	Females
Natural sciences	68	77
Social studies	87	86
Arts, letters and philosophy	67	58
Total	222	221
		No. of Families = 191
		$p = .56$
FIRST-BORN		
	Males	Females
Natural sciences	33	31
Social studies	35	38
Arts, letters and philosophy	30	24
Total	98	93
		$p = .73$

tested, after eliminating names of Grant subjects. Special studies had been made upon this class during its freshman year in college (1939) including a shortened somatotyping by C. C. Seltzer. Sex of offspring was obtained from the class tenth reunion report. Table 4 shows again the lowered sex ratio for the predominantly mesomorphic, and table 5 shows the same curious relationships between sex ratio and field of concentration. When ratios were determined only for first-born offspring, the same consistencies were found; in fact, the described trends seem to be stronger for first-born than for second- or third-born. Utilizing the first-born, of course, eliminates any possible influence or bias family size might have upon the statistics.

TABLE 4

*Control: Class of 1943 minus Grant Men; mesomorphy and sex ratio of offspring*

ALL CHILDREN			
	Males	Females	
Mesomorphy predominant	202	192	No. of Families = 413 p = .33
“ not predominant	246	204	
Total	448	396	
FIRST-BORN			
Mesomorphy predominant	85	101	p = .08
“ not predominant	124	103	
Total	209	204	

TABLE 5

*Control: Class of 1945 minus Grant Men; college field of concentration (major) and sex ratio of offspring*

ALL CHILDREN			
	Males	Females	
Natural sciences	164	164	No. of Families = 418 p = .22
Social sciences	171	149	
Arts, letters and philosophy	117	85	
Total	452	398	
FIRST-BORN			
Natural sciences	79	85	p = .65
Social sciences	84	74	
Arts, letters and philosophy	51	45	
Total	214	204	

Table 6 shows, in abbreviated form, the selected results of comparison between various factors and sex ratio of offspring. While mesomorphy and ectomorphy have shown relations to sex ratio, the third element of fatness (edomorphy in Sheldon's somatotyping) has repeatedly given equivocal results when compared with sex of offspring. It is possible that this accounts somewhat for the relative lack of influence of  $Ht./\sqrt[3]{Wt.}$  upon sex ratio for these groups. Men with  $Ht./\sqrt[3]{Wt.}$  of 13.0 or less in the

TABLE 6  
*Other factors and sex ratio of offspring*

Factor Present in Father	Series	Sex of Offspring		Sex Ratio	p *
		No. Males	No. Females		
Predominant ectomorphy	Grant	50	43	1.16	.08
" "	Class of '43	127	114	1.11	.99
" cerebrotonia	Grant	125	100	1.25	.02
$Ht./\sqrt[3]{Wt.}$ 13.0 or less	Grant	110	127	0.87	.18
" "	Class of '42	93	101	0.92	.48
" "	Class of '43	242	213	1.14	.99
Large tidal air (600 cc or more)	Grant	83	108	0.78	.08
Recovery index, 65 or more	Grant	70	94	0.74	.05
Major in Engls and language	Grant	52	42	1.24	.25
" " " " "	Class of '43	86	67	1.28	.45
" " chem., physics, math.	Grant	54	61	0.89	.45
" " " " "	Class of '43	93	109	0.85	.47
Labelled by trait: practical					
" " " organizing	Grant	71	102	0.70	<.01
" " " : cultural	Grant	51	32	1.59	.02
Weak masculine body build	Grant	81	76	1.07	.46
" " " "	Class of '43	50	42	1.19	.42

\* By the Chi-square Test, usually a  $2 \times 2$  table being used, comparing offspring of men possessing the factor with those of men not possessing it.

Class of 1943 had about the expected sex ratio of their offspring. However this factor is available for other classes and was tried with the Class of 1942, showing a consistent reduction of sex ratios for fathers with low  $Ht./\sqrt[3]{Wt.}$  A large tidal air (volume of air per inspiration at rest) is found somewhat more commonly in the more athletic and mesomorphic young men than among their opposites and was used for further com-

parisons. "Recovery index" is a measure of physical fitness for hard muscular work, higher scores indicating higher fitness (Johnson *et al.*, '42). Although  $p$  is only occasionally .05 or less, the figures are consistently in the expected direction. The relationship of these various factors with sex of offspring is consistent with the hypothesis: muscular and active fathers tend to have more daughters than sons; thin and intellectual fathers tend to have more sons than daughters. That the phenomenon is more complex than this is suggested by the last item in table 6: weak masculine body build (Seltzer, '45). Such individuals are not thin usually, but they tend to have more boy than girl babies.

It is suggested that some common factor may be acting in the body to modify both physique and temperament and the sex of the offspring. It is hoped that interested observers will pursue these studies for other and larger groups. It would seem, however, that the most fruitful inquiry might be among known biochemical body constituents which may be related to physique and temperament. No definitely corroborative work has been found in the literature. In a personal communication E. E. Hunt, Jr. says that the findings are in accord with some which he has made on the people of the island of Yap. No comparable long-term data are available for women.

### LITERATURE CITED

- HEATH, C. W. *et al.* 1946 What People Are. Harvard University Press, Cambridge, Massachusetts.
- JOHNSON, R. E., L. BROUHA AND R. C. DARLING 1942 A test of physical fitness for strenuous exertion. *Revue canadienne de Biol.*, 1: 491-503.
- SELTZER, C. C. 1945 The relationship between the masculine component and personality. *Amer. J. Physical Anthropol.*, n. s. 3: 33-47.
- SELTZER, C. C., F. L. WELLS AND E. B. MCTERNAN 1948 A relationship between Sheldonian somatotype and psychotype. *J. of Personality*, 16: 431-436.







# PHYSICAL DEVELOPMENT IN THE ENGLISH AND THE AMERICAN PRE-SCHOOL CHILD

## A COMPARISON BETWEEN FINDINGS IN THE OXFORD AND THE BRUSH FOUNDATION SURVEYS<sup>1</sup>

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### INTRODUCTION

THE most widely used method of assessing the skeletal maturity of a child is to compare a radiograph of its hand with a series of standard films which have previously been chosen as typical of various ages. The standard films generally used for this purpose are those published by Todd ('37) in his *Atlas of Skeletal Maturation* and in the revised version of this atlas by Greulich and Pyle ('50). Since the films in these atlases were chosen to be typical of a group of well-to-do, white children reared in one district in the U. S. A. "there is no reason to expect that they will fit exactly any other group. . . . But standards do not have to fit exactly in order to provide an adequate assessment of skeletal status. They can be somewhat or even much advanced or retarded as compared with the rate of skeletal development of a group of children to whom they are applied, and still permit one to determine how the skeletal status of any child in that group compares with the others of his age and sex, as well as with the children on whom the standards are based." (Greulich and Pyle, '50). In a previous study Todd's atlas was used to assay some factors influencing the skeletal maturation of children in the Oxford Child Health Survey (Acheson and Hewitt, '54). In this paper the same atlas has been used to compare the maturation of these English children at Oxford with that of American children in the Brush Foundation Study at Cleveland.

<sup>1</sup> The Oxford Child Health Survey has been financed by grants from the Medical Research Council and the Nuffield Provincial Hospitals Trust.

## MATERIAL

The purpose of the Oxford Child Health Survey was to keep under continuous observation, for a period of 5 years, 500 babies born in or near the city after January 1, 1944, and to obtain for these children serial records of interest to clinicians and social workers. A special effort was made to recruit children from all economic levels. This is in sharp contrast with the selection practised in the Brush Foundation Study where "the intention was to confine this sampling to children who would be reasonably free from physical, mental and nutritional handicaps to that growth and development pattern normal for each child; to children who would be reasonably free, that is, from environmental handicaps to the realization of their inherited potentialities," (Simmons, '44). Thus the Oxford Survey sought to examine the effect of an environment on development, while the Brush Study aimed at describing the process of development in an optimal environment.<sup>2</sup>

At the age of 6 months, and at 6-monthly intervals thereafter, X-rays were taken of the chest, of both hands and both knees. In addition each child had one of the following anatomical parts X-rayed: spine, skull, feet or pelvis. About 90% of the hand X-rays were assessed by an expert radiologist, the remainder by his trainee (R. M. A.) who repeatedly checked his own and his instructor's assessments. All assessments were made to the nearest Todd standard, i. e., to the nearest whole three months of "skeletal age" for the first year and a half of life and thereafter to the nearest whole 6 months. It was felt that any attempt to interpolate within these limits might lead to spurious accuracy. This degree of approximation does not affect the comparison of English and American mean values, but makes it inappropriate to compare standard deviations of skeletal age.

*Maturation of English Children compared with Todd's Standards*

The first step in the analysis was to see whether or not the skeletal development of the Oxford children conformed to the general pattern of the Todd atlas ('37). It was not to be expected that the mean skeletal

<sup>2</sup> Since the methods, as well as the dates, of recruitment differed so much between the surveys these samples must not be regarded as equally representative of conditions in England and America. Though we have found it convenient to refer to "the English children" and "the American children" we do not wish to claim that we have made any valid comparisons of general standards of development in the two countries.

age of the Oxford children would be identical with their calendar age, nor even that any difference between the two would remain constant throughout childhood. But the mean skeletal age of any group of healthy children should, by definition, bear a linear relationship to the mean calendar age. When these two quantities were plotted against one another, it was found that the points for boys could be adequately

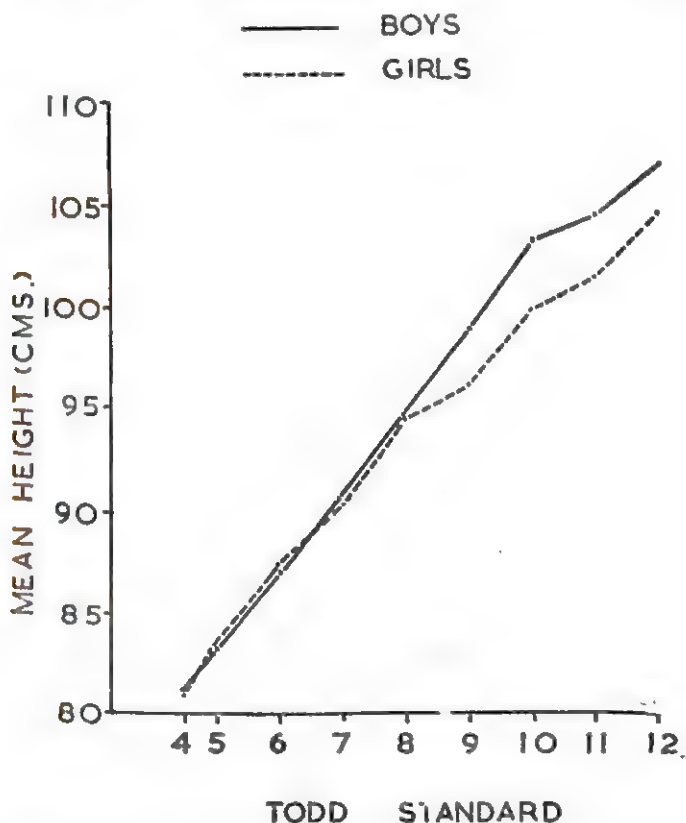


FIG. 1. HEIGHT OF OXFORD BOYS AND GIRLS RELATED TO TODD'S STANDARDS OF SKELETAL MATURITY.

represented by a straight line, thus confirming that the Todd standards were applicable to Oxford boys. But the points for girls appeared to follow a curve concave towards the skeletal age axis. That is to say, there was a tendency for the maturation of these girls to accelerate relative to the Todd standards. This could have been due either to a peculiarity in the rate of development of the Oxford girls or to a fault in the standards themselves. Figure 1 suggests that the latter is the more likely alternative.

In this figure are plotted the mean heights of all boys and all girls observed at each of the Todd standards from the fourth to the twelfth. At standards Four to Eight inclusive there are only trivial differences in height between the sexes. Between standards Eight and Nine the boys grew at the same rate as before, while the girls appeared to grow only half as much. From standard Nine onwards the two sexes were again very similar in rate of growth. The difference between the sexes which figure 1 seems to show is so abrupt and short-lived that it must be regarded as an artificial effect, and may result from an error in making the female standards Eight and Nine too similar to one another. Apart from this one flaw, however, there seems no reason to question the applicability of the Todd standards to the boys and girls of Oxford.

*Growth and Maturation of Oxford Children compared with that of  
Brush Foundation Children*

The data on skeletal maturity of American children used in this section are those based on Todd's atlas ('37) but which were published by Greulich and Pyle ('50) in the introduction to their work. Standing heights of the same children have been taken from the monograph by Simmons ('44). In both the Oxford and the Brush surveys the two-year examination was the earliest at which all the children were able to co-operate in the measurement of stature. A large proportion of them had, however, been satisfactorily measured at the age of 18 months, and most of the comparisons which follow cover the age range one and a half to 5 years.

In tables 1 and 2 the mean heights of the Oxford boys and girls are set against the corresponding means for the Brush Survey children. It will be seen that in every case the Oxford children were shorter than the American children of the same age. The height difference, in absolute measure, increased from about 7 mm at 18 months to about 22 mm at the age of 5. The lag of the Oxford children also appeared to increase from approximately one-quarter to one-half of a standard deviation.

A small part of the difference between the findings of the two surveys may be due to the fact that the American children who were "dressed in indoor clothing, shoes removed" (Simmons, '44) presumably wore socks at the time of measurement, whereas the English children were measured barefoot. A second reason for differences can be inferred

TABLE 1  
*Height of Oxford and Brush survey boys*

Calendar Age (months)	Oxford Survey			Brush Survey			Deviation of Oxford Mean from Brush Survey Mean		
	No. of boys	Mean Height (mm)	S. D. (mm)	No. of boys	Mean Height (mm)	S.D. (mm)	In S. D.		
							In mm	(Brush) units	
18	135	812.55	32.97	99	818.62	26.74	—	6.07	—0.23
24	254	865.38	35.26	164	874.10	31.80	—	8.72	—0.27
30	240	907.80	36.65	170	922.18	31.81	—	14.38	—0.45
36	242	949.96	40.61	195	963.64	34.46	—	13.68	—0.40
42	239	989.84	42.90	193	1002.56	35.65	—	12.72	—0.36
48	243	1023.11	44.07	216	1039.83	36.20	—	16.72	—0.46
54	225	1057.66	43.79	213	1075.89	38.74	—	18.23	—0.47
60	234	1088.90	48.13	225	1106.71	40.48	—	17.81	—0.44

TABLE 2  
*Height of Oxford and Brush survey girls*

Calendar Age (months)	Oxford Survey			Brush Survey		Deviation of Oxford Mean from Brush Survey Mean	
	No. of girls	Mean Height (mm)	S. D. (mm)	No. of girls	Mean Height (mm)	In S. D. (Brush) units	
						In mm	(Brush) units
18	129	792.73	32.82	95	800.40	33.33	- 7.67
24	262	846.07	32.28	165	860.85	31.85	-14.81
30	259	894.33	36.91	166	911.34	33.42	-17.01
36	263	935.74	36.78	186	953.99	35.69	-18.25
42	246	976.88	36.86	192	995.26	36.18	-18.38
48	250	1012.95	38.91	222	1033.02	37.45	-20.07
54	238	1045.72	40.59	218	1071.81	42.66	-26.09
60	238	1079.75	43.61	225	1106.42	43.71	-26.67



from the figures in tables 1 and 2. These show that compared with Americans of the same age, English children tended to be in a slightly earlier phase of height gain. During the years covered by these tables, girls, who are distinctly shorter than boys in infancy, gain one or two centimeters more in height than do boys. This tendency for the heights of the sexes to converge means that, of any two groups of children, the

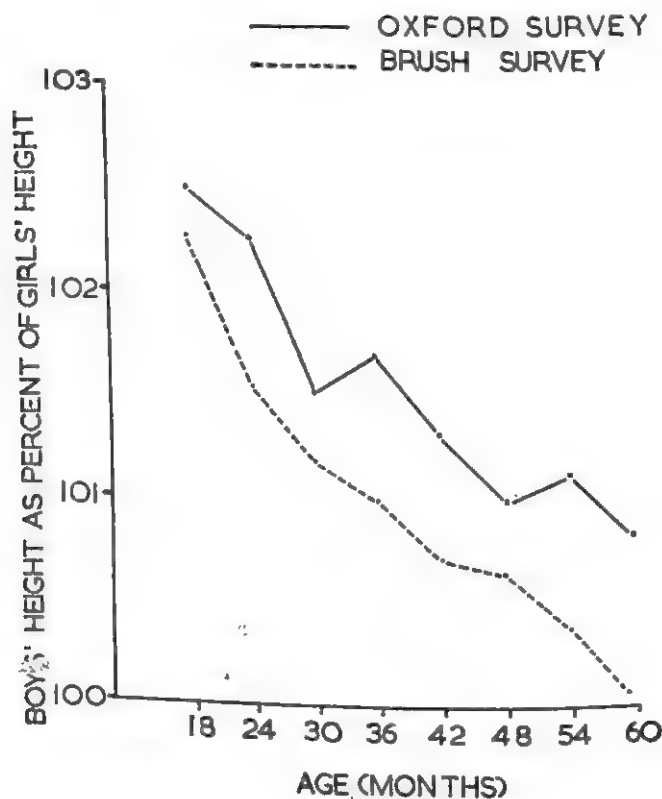


FIG. 2. MEAN HEIGHT OF BOYS AT VARIOUS AGES AS A PERCENTAGE OF THE CORRESPONDING MEAN FOR GIRLS.

one with the *smaller* excess of male over female height is at a more advanced stage of physical development and nearer to final, adult height. Figure 2 shows that, by this criterion, the children of the Brush Survey were well ahead of the Oxford children. This implies that a comparison of the English and the American heights based on equally mature children would be more favorable to the English children than the comparisons made above.

There is one further point in tables 1 and 2 which deserves comment. It will be noticed that the standard deviations of the heights recorded in Oxford were greater than those found in the Brush survey and that this excess is more characteristic of the boys (with a standard deviation averaging about 18% wider than the American boys) than of the girls (standard deviation only about 2% wider than the American girls). This is interesting in view of Parnell's observation that an economically favored group, as well as being tall, has an unusually compact height distribution (Parnell, '51). It also accords with the suggestion that, when comparisons are made between children of equal calendar age, environment has more effect on the heights of boys than of girls (Greulich, '51; Greulich, *et al.*, '53; Acheson and Hewitt, '54).

In tables 3 and 4 the mean skeletal ages reached by the Oxford boys and girls are compared with those reached by Brush Survey children of equal age. Once again the English children (of both sexes and at all ages) appear to be lagging behind the Americans. At the age of one and a half the English boys were 5 "skeletal months" behind; at the age of 5 the gap had widened to about 8 "skeletal months." In terms of the (American) standard deviation the skeletal maturity of the English boys was considerably more retarded than their size. While the height difference, measured in standard deviations, was increasing with age (see table 1 above), the maturity difference was decreasing. At the age of one and a half the English girls were about 5 "skeletal months" behind, but thereafter they showed no tendency to lose ground so that, in terms of the standard deviation, they were closing up on the Americans more rapidly than the boys.

The evidence of tables 3 and 4 strengthens the inference drawn from figure 2 that the English children tended to be in an earlier phase of physical development than American children of equal age. This relative immaturity of the English children may be regarded as a second aspect of general physical backwardness, possibly due to a sub-optimal environment for a growing child. In the long run, however, some degree of skeletal retardation may prove an asset to children whose growth is slow. For the longer the period that remains before the final closure of the epiphyses the more chance there is of catching up in height with other, more rapidly developing children.

In view of these findings it is reasonable to compare the mean heights of the Brush sample as a whole with the mean heights from other surveys on the basis of equal skeletal ages as well as equal calendar

TABLE 3  
*Skeletal maturity of Oxford and Brush survey boys*

Calendar Age (months)	Oxford Survey		Brush Survey		Deviation of Oxford Mean from Brush Survey Mean	
	No. of boys	Mean skeletal age (months)	No. of boys	Mean skeletal age (months)	Mean skeletal age (months)	In S. D. (Brush) units
18	298	14.4	106	19.36	3.52	-4.96
24	293	21.1	105	25.97	3.92	-4.87
30	248	26.6	107	32.40	4.52	-5.80
36	247	32.9	127	38.21	5.08	-5.31
42	242	37.5	138	43.89	5.40	-6.39
48	244	42.0	170	49.04	6.66	-7.04
54	225	48.5	176	56.00	8.36	-7.50
60	234	53.9	191	62.43	8.79	-8.53

TABLE 4  
*Skeletal maturity of Oxford and Brush survey girls*

Calendar Age (months)	Oxford Survey		Brush Survey		Deviation of Oxford Mean from Brush Survey Mean	
	No. of girls	Mean skeletal age (months)	No. of girls	Mean skeletal age (months)	In months	In S. D. (Brush) units
18	289	13.5	93	18.22	3.49	-4.72
24	289	18.6	101	24.16	4.64	-5.56
30	263	24.9	98	30.96	5.37	-6.06
36	263	32.9	133	36.63	5.97	-3.73
42	248	37.5	131	43.50	7.48	-6.00
48	252	45.7	154	50.14	8.98	-4.44
54	239	53.1	152	60.06	10.73	-6.96
60	235	60.9	167	66.21	11.65	-5.31

ages. This has been done in figure 3 where the mean height of each age-group is plotted, not against the age itself but against the corresponding mean skeletal age. These graphs should be thought of as having a limit on the skeletal age scale at 225 "skeletal months" for boys and 195 for girls. After reaching the limit there can be no further increase

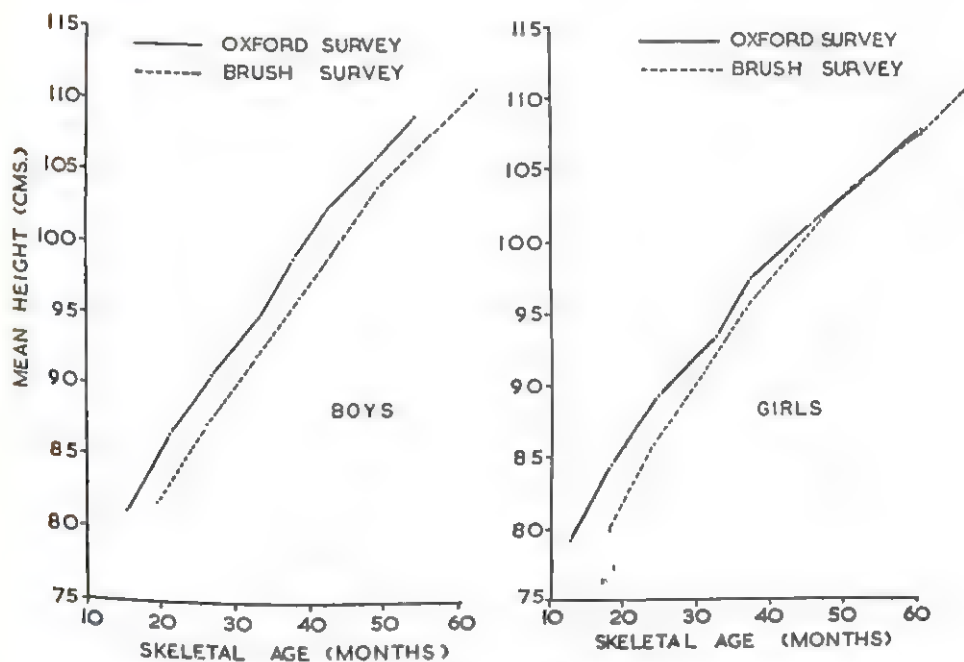


FIG. 3. RELATION BETWEEN HEIGHT AND SKELETAL AGE.

of skeletal age or of height. The Oxford data only cover the first third of the range, so that it is not possible to make any confident statements about the final heights of the English children. There is, however, a *prima facie* case for regarding the group who are represented by the highest line on such a graph as potentially the tallest. In figure 3 the line for English boys lies distinctly higher than that for American boys; the line for English girls is at first higher than and then indistinguishable from that for American girls. Thus the height and maturity comparisons which, taken separately, show the English children as a relatively backward group also imply, when they are taken together, that

the English children may become as tall or even taller than the Americans in adult life. It would, however, be unwise to accept this finding at its face value, since:

(1) The two samples were not observed contemporaneously.

(2) Relationships between environment and development which obtain during the first 5 years of life do not necessarily persist through later childhood and adolescence.

(3) The methods of comparison so far adopted are particularly vulnerable to any systematic bias in the recording of height or of skeletal age in either the English or the American data.

Should any such bias run through the records it can be eliminated (provided it takes the form of a constant absolute error) by making the international comparison in terms of increments instead of absolute amounts. This is shown in table 5 which sets out the differences between the two year<sup>3</sup> and the 5-year means for height and for stage in each survey.

TABLE 5

*Increase in height and skeletal maturity of Oxford and of Brush survey children between the ages of two and five years*

		Oxford Survey increase	Brush Survey increase	Oxford increase as percentage of Brush increase
<i>Height</i> (mm)	Boys	223.52	232.61	96%
	Girls	233.68	245.57	95%
<i>Skeletal Maturity</i> (months of skeletal age)				
	Boys	32.3	36.4	90%
	Girls	42.3	42.0	101%

Over this age range the Oxford children of both sexes gained about 5% less in height; in skeletal maturity the Oxford boys gained about 10% less while the girls gained equally in the two surveys. It would be more instructive to make the comparisons of height gain over a period of development defined by skeletal rather than calendar ages. This can

<sup>3</sup> The age of two was taken rather than one and a half because of the greater numbers available.



be done, but we must be prepared to ignore the possibility of errors arising from bias in the recording of skeletal age (systematic errors in the heights are assumed not to affect height increments). The appropriate procedure is illustrated in table 6. This table shows that between the

TABLE 6

*Increase in height of Oxford and of Brush survey children: Comparison made over same phase of skeletal maturation*

		Oxford Children		Brush Children
		Height	Skeletal Age	Height interpolated * at corresponding skeletal age
Boys	Age 2	865.38	21.1	833.22
	Age 5	1088.90	53.9	1065.01
	Increase	223.52	—	231.79
	% of Brush Increase	96.4%	—	100.0%
Girls	Age 2	846.07	18.0	804.27
	Age 5	1079.75	60.9	1076.54
	Increase	233.68	—	272.27
	% of Brush Increase	85.8%	—	100.0%

\* Interpolation by proportional parts between adjacent points e.g. boys aged two:  $818.62 + \frac{21.1 - 19.36}{25.97 - 19.36} (874.10 - 818.62)$ .

21st and 54th "skeletal months," Oxford boys were estimated to gain 96% of the height gained by the Brush boys; while the Oxford girls, between the 19th and 61st "months" were estimated to gain only 86% of the height gained by the Brush girls. Thus the rate of increase in height per unit increase in skeletal maturity (on which adult stature ultimately depends) was greater for the American boys and girls than for the English children. The English girls appeared to be relatively further behind than the boys, not so much because their rate of growth relative to time fell any further short of the American standard, but because, unlike their brothers, these English girls matured as rapidly as the Americans.

#### DISCUSSION

Todd referred to the age associated with any standard radiograph as the "skeletal age" of the child concerned, and established the convention of treating skeletal ages as if they were points on some absolute scale of skeletal maturity. In fact no such scale has yet been devised,

and the student of maturation is still in a position which may be likened to that of a student of weight gain who has been equipped with a balance but cannot put more than one object in each pan. By a series of balancing experiments he can identify the median child in each age-group, and then, using these children as his weight standards, he can estimate what he might call the "ponderal age" of the other children. He could then compare the mean ponderal ages of different racial or economic groups and reach some valuable conclusions. But he could never discover, for example, those phases in childhood when weight gain is relatively fast or slow. Elsewhere one of us (Acheson, '54) has criticized the concept of skeletal age, suggested an alternative method of assessing radiographs, and applied this to the hand and knee films of the Oxford children. For the purpose of comparison with the Brush Foundation children it is, however, necessary to adopt the only method of assessment which has been applied in both surveys, and with it Todd's concept of skeletal age.

The comparisons made in this paper are complicated by the fact that the two groups of children were of different stock. Though the American children were all white and the majority of them were of North European descent, their racial antecedents were probably more mixed than the Oxford group, who were mostly English with the usual admixture of Irish and Scottish ancestry. It may be, therefore, that the children of one of the samples had a greater inherited potentiality for growth, or that there was some difference in their natural mean rates of maturation.

The contrast in environment is less problematic. On average, the environment and home circumstances of the American children must have been more favorable because of the different methods by which the two samples were selected.<sup>4</sup> Therefore any difference between the English and the American children which can be paralleled by a difference between poorer and richer children within the English sample may plausibly be regarded as an effect of differing environments. In fact three findings of the present paper parallel the findings in our previous study of growth and maturation in contrasted economic strata of Oxford (Acheson and Hewitt, '54):

(1) In both studies the boys and girls who grew up in the worse environment were shorter than other children of the same calendar age. The difference between the average height of the Oxford and the

<sup>4</sup> See footnote 2.

Cleveland samples was of the same order of magnitude as the difference between children of unskilled and of professional parents in Oxford.

(2) In both studies the boys from the worse environment were skeletally less mature than other boys of the same calendar age. Here the Oxford-Cleveland difference was rather greater than the social class difference. In both studies environment appeared to have less effect on the maturation of girls than on that of boys, for the Oxford-Cleveland difference in maturity was slightly less for girls than for boys, and in the social class comparison no effect on the maturation of girls could be detected at all.

(3) Comparison of the children on the basis of equal skeletal age (rather than equal calendar age) suggested that the effect of environment on final stature might be greater for girls than for boys.

Comparisons of Guamanian with Cleveland children (Greulich, '51), and of children exposed to atomic bombing with other Japanese children (Greulich, *et al.*, '53) also bear out findings (1) and (2).

#### SUMMARY

The physical development of approximately 500 Oxford children, from different economic levels, followed over the first 5 years of life, is compared with that of the Brush Foundation children. On average the English children are shorter and less skeletally mature (Todd). In order to avoid systematic error arising from possible differences in anthropometric technique, increments are studied. The English increments as a percentage of the American are estimated as:

- (1) Stature increase per unit time: boys 96%, girls 95%.
- (2) Skeletal maturity increase per unit time: boys 90%, girls 101%.
- (3) Stature increase per unit skeletal maturity increase: boys 96%, girls 86%.

These findings parallel those found between the different economic strata within the Oxford Survey.

## LITERATURE CITED

- ACHESON, R. M. 1954 A method of assessing skeletal maturity from radiographs: a report from the Oxford Child Health Survey. *J. Anatomy* (London), 88: 498-508.
- ACHESON, R. M., AND D. HEWITT 1954 Oxford Child Health Survey: Stature and skeletal maturation in the pre-school child. *Brit. J. Prev. Soc. Med.*, 8: 59-65.
- GREULICH, W. W. AND S. I. PYLE 1950 Radiographic Atlas of Skeletal Development of the Hand and Wrist. Stanford University Press. Stanford, Calif.
- GREULICH, W. W. 1951 The growth and developmental status of Guamanian school children in 1947. *Am. J. Phys. Anthropol.*, n. s. 9: 55-70.
- GREULICH, W. W., C. S. CRISMON AND M. L. TURNER 1953 The physical growth and development of children who survived the atomic bombing of Hiroshima or Nagasaki. *J. Pediat.*, 43: 121-145.
- PAENELL, R. W. 1951 The Health of Undergraduates. D. M. Thesis (unpublished) Bodleian Library, Oxford, England.
- SIMMONS, K. 1944 The Brush Foundation study of child growth and development: II. Physical growth and development. *Soc. Res. Child Dev. Monog.*, 9: Washington.
- TODD, T. W. 1937 Atlas of Skeletal Maturation—The Hand. Mosby and Co., St. Louis.



## BOOK REVIEWS

*The Fourth Mental Measurements Yearbook.* Edited by O. K. BUROS, 1163 pp., the Gryphon Press, Highland Park, New Jersey, 1953, \$18.00.

While the development of new tools for mental measurement is a highly technical job, standardized "mental tests" have a wide usage in research in a variety of segments of human biology as well as a practical application in educational, industrial, military, and psychiatric contexts. It is the aim of the *Yearbook*, and of its six predecessors, to assist the potential test users in locating and evaluating tests and books on testing published from 1948 through 1951.

The successive editions, each containing new materials and thus supplementing rather than supplanting the earlier volumes, have been growing steadily in size and in the number of items reviewed. The first section of the present edition covers some 800 tests. In addition to the reviews of tests which had been already published in a wide array of journals, there is a large number of reviews written specifically for the *Yearbook*. For purposes of orientation it may be useful to group the tests in 5 categories: sensory-motor (20 pp.), intelligence (112 pp.), character and personality (226 pp.), aptitudes and achievement (reading, English, foreign languages, fine arts, mathematics, science, social studies, achievement batteries, vocations) and the unavoidable "miscellaneous" left-overs (accounting together for some 460 pages of the text). There are over 4,000 references to publications dealing with the construction, validation, and use of the tests.

The second section contains titles and, in most instances, reviews of over 400 books. Some books are reviewed by several authors. This adds up to a total of 758 book reviews taken, in part or *in toto*, from 121 journals. No original book reviews were solicited for this section. The use of the massive volume is facilitated by three indexes, as well as the directory and index of periodicals and publishers.

In the days characterized by an overabundance of books and papers in almost any field of scientific endeavor, synthesizing efforts are badly needed to register and evaluate the "output." In the field of mental measurement, Buros' *Yearbooks* have served this purpose well. For the



future, in which the output may be expected to continue high, a more selective attitude may be the only way to save this valuable enterprise from collapse due to the sheer weight of the material and reduced sale volume resulting from a high price. Even now, while the volume should certainly find its way to all the libraries in which a comprehensive reference book on the tools and theories of psychological testing is needed, the individual user may pause before making out so large a check even though he would *like* to have the book on his shelf.

JOSEF BROŽEK

*The African Mind in Health and Disease; A Study in Ethnopsychiatry*, by J. C. CAROTHERS. 177 pp. World Health Organization, Geneva, Monograph No. 17, 1953. Paper bound, \$2.00.

Readers of *Human Biology* will find fascinating this well written monograph incorporating the contributions of anthropology, sociology, psychology, psychiatry, human physiology, pathology and nutrition to the study of the mind of the African.

Of Africa's 170,000,000 native people, about 110,000,000 are Negroid, living south of the Sahara Desert and long isolated, genetically and culturally. This is a unique phenomenon, of particular interest to students of man's mental apparatus. For this reason, the World Health Organization thought it worthwhile that a review and commentary be written on this subject and commissioned Dr. Carothers to do so. The author was reared in South Africa and worked for 21 years in Kenya. Of this time, 1½ years were spent at the mental hospital in Nairobi.

The monograph consists of three sections: I. The Physical Background of the African; II. The Mind of the African; and III. Discussion on Evolution and Culture.

First, the author defines in the dimensions of anthropology, genetics, geography, and climatology the peoples of his study. They live in a vast, inaccessible region of low population density, subject to intense solar radiation, fluctuation between ill-spaced rains and drought, and on soil generally deficient in calcium and phosphorous. Attention is directed to the effects of genetic, infectious, deficiency, endocrine, neurological, hematopoietic and addictive diseases. The cultural conditions under which the African develops are characterized in the oral period by prolonged, extraordinarily indulgent nursing, ending abruptly between the 24th to 36th month; in the anal-muscular period by the absence of

social training, with answers to "why" being given in magical animistic absolute terms which stifle curiosity; and in the oedipal period by uninhibited childhood sexual play. Due to an absence of toys, manipulative skill and form perception is not developed. By adolescence, processes favoring individualistic development have ceased and pressures to fit into a rigid static social framework become dominant. In adulthood, the behavior patterns are fixed, and "life is governed by rules and taboos which are meticulously anchored to the land. Free expression is limited to oratory, music, dance, and the weaving of fairy tales." Super-ego is but slightly internalized, the deterrent to aberrant action lying not within the individual but within the public opinion.

To disentangle the parts that constitutional and environmental factors play in producing distinctive characteristics in the mentality of the African, the author proceeds to describe what studies have been made and to assess their merits from the viewpoint of his own multidisciplinary perspective. The African has been described as "conventional; highly dependent upon physical and emotional stimulation; lacking in spontaneity, foresight, tenacity, judgment and humility; inapt for sound abstraction and logic; given to phantasy and fabrication, and, in general, as unstable, impulsive, unreliable, irresponsible, and living in the present without reflection or ambition, or regard for the rights of people outside his own circle. To counteract these ruderies, he has also been described as cheerful, stoical, self confident, sociable, loyal, emotionally intuitive and eloquent, and as bearing no grudges and having an excellent memory, a large vocabulary and an aptitude for music and the dance."

Chapter VII, on "Psychology in Relation to Environment" is excellently presented. Its main theme is that preliterate African man has through hundreds of generations developed a culture along such lines as to "reduce the exigencies of living to a minimum so that the integration which the rural African apparently achieves is founded on the continuing support afforded by his culture to the end that he has but little independent existence in himself." Superimposed upon these basic traits are the deleterious effects of malnutrition and disease which in turn may at various times influence the patterns of his culture.

Included in the monograph is a long, interesting chapter on psychopathology. Emotions easily dominate the African's mind. Stresses are not handled intrapsychically by neuroses, as known to Europeans, but by the rules, laws and taboos of the social framework. Psychoses have their structure so altered by lack of strong integrational patterns in the

ego that they assume amorphous and abortive forms. With vitality, drive and individual maturation severely affected by malnutrition and disease, solution of the nutritional and infection problem is a prerequisite for establishing and maintaining efficient mental function.

J. VICTOR MONKE

*Catalogue des Hommes Fossiles*. Edited by HENRI V. VALLOIS and HALLAM L. MOVIUS, JR. Reprint, Fasc. V Comptes Rendus XIX<sup>e</sup> Congrès Géologique International. Alger, 1952, pp. 59-378 (1-320). Francs 500.

The present catalogue constitutes a complete record of all fossil human remains known to exist or described up to the year 1952. W. & A. Quenstedt's *Fossilium Catalogue. Hominidae Fossiles* (W. Junk, The Hague, 1936) brought the material up to 1935, but this excellent work was so costly that its circulation was severely restricted. F. Hue's *Crânes Paléolithiques* (Société Préhistorique Française, Paris, 1937) which brought the material up to the year 1936, for some reason seems to have enjoyed an even narrower circulation. During the last 20 years many important discoveries of fossil hominid and hominoid remains have been made, so that an up-to-date catalogue has been a desideratum.

With the aid of 33 collaborators the editors and the Union Paléontologique Internationale have put all students of fossil man deeply in their debt by providing the essential data concerning site, discoverer, type of industry, principal associated fauna, geology and archeology, character of the remains, repository, casts available, and bibliography. Illustrations have been omitted for the simple reason that they would disproportionately have increased the cost of a volume which without them is easily within the reach of any student desiring a copy.

It is very much to be hoped that this excellently produced and useful work will have a long life, and that from time to time new editions of it will appear.

Copies of the work may be obtained at the price of 500 francs from: Secrétariat Général, XIX Congrès Géologique International, Faculté des Sciences, Alger, French North Africa.

ASHLEY MONTAGU

*An Rh-Irr Syllabus.* By A. S. WIENER. xii + 82 pp. Grune & Stratton, New York, 1954, \$3.75.

Time was when a non-specialist, with an ordinary amount of application, could keep abreast of the work in blood grouping and typing. But progress in this branch of serology has of late years been so rapid that it has become virtually a full-time job to keep up with the new discoveries and the increasing complexity of the subject.

In the present volume, Wiener sets out to put the inexpert reader at his ease with the Rh-Irr types. His object of presenting a compact, readable, up-to-date summary of the subject is accomplished by presenting the information in the form of a glossary, arranged in logical rather than alphabetical order.

Following an account of the fundamentals of the subject, the author proceeds to a discussion of the Rh antibodies, the serology and genetics of the Rh-Irr types, erythroblastosis fetalis, blood transfusion, and auto-sensitization. He also discusses the anthropological and medico-legal aspects of the subject, and there is a useful index.

Wiener's discussion and criticism of the Fisher symbols for Rh phenotypes, his classification of ethnic groups, and his suggested explanations of the mechanisms involved in various obscure hemolytic conditions add to the interest as well as the value of this little volume.

The clarity of the diagrams and the tables combine to ease the reader's path. The volume would benefit from the dropping of a few solecisms in a future edition.

ASHLEY MONTAGU

*Clinical Genetics.* Edited by ARNOLD SORSBY. xi + 580 pp. C. V. Mosby Co., St. Louis, Missouri, 1953, \$17.50.

This volume constitutes a substantive contribution to clinical pathology from the standpoint of genetics. It is a book which all human biologists will at some time wish to consult. Altogether there are 29 contributions by 26 contributors. The book is divided into two sections. (I) Theoretical Considerations, and (II) Clinical. An elementary knowledge of genetics is assumed throughout.

Sorsby opens with a discussion of "Clinical varieties of disease," which is admirable for its balance, its emphasis on heredity as the interaction between genotype and environment, and its extremely valu-

able "tentative classification of the clinical varieties of genetic disease." Snyder and David follow with by far the best discussion of "Penetrance and expression" that we have. Here these authors also enter upon a valuable account of modifying environmental factors, and a discussion of the constitutional approach, which make an admirable supplement to Sorsby's article and a good introduction to those which follow. Neel's "The detection of genetic carriers of inherited disease," offers both an able discussion and a useful table of the carrier states of 33 diseases and their probable mode of inheritance. Waterhouse summarizes "Twin studies" in a paper which is a model of its kind. Ford's discussion of "Sex limitation" represents an important contribution toward the clarification of a too often confusedly discussed subject. Mather's "Polygenic inheritance" is a magisterial piece, treating of a highly complex subject, the statistical genetics of continuous variation, with consummate ease and clarity. Macgregor provides a crystal-clear "Evaluation of linkage," which is at once theoretically enlightening and practically helpful. Crew's informative chapter on "Mutation" contains a section on "Medical and social aspects of mutation" which is of the first order of importance and should be required reading by all human biologists. Dahlberg's exposition of the "Biometric evaluation of findings" is almost certainly the best short piece of its kind; indeed, it is a masterpiece. Koller's admirable account of "Cytogenetics" contains a grave warning which reinforces the comments of Crew. In discussing the potential dangers of radiotherapy and chemotherapy, Koller urges the greatest caution and continuous investigation, for, as he says, "Gene mutations are almost always deleterious and if they are produced with high frequencies, they will, throughout future generations, kill more people whose germ plasma is contaminated with the mutated genes than could be killed directly by the explosion of the atom bomb" (p. 119). Catchside is quite exciting on "Chemical genetics." With a section on "Comparative pathology" Sorsby concludes the first part of the volume.

Part II opens with a discussion by Tanner of the "Inheritance of morphological and physiological traits." D. Klein presents an able analysis of "Metabolic disorders," and O. L. Scott deals with "Diseases of the skin"—the largest and physiologically least studied of the organs of the human body. In an admirable article Falls deals with the "Skeletal system, including joints." Stephens on "Muscular disorders" is excellent. Pratt on "Diseases of the nervous system" deals most ably with a difficult subject, and Böök on "Oligophrenia" (mental deficiency)



is both informative and well-balanced. Slater on "Psychiatry" is exemplary. Every psychiatrist would benefit greatly from a reading of this remarkable paper. His discussion of the strengths and weaknesses of psychiatric genetics should be read by all human biologists. Somewhat surprisingly Slater rather uncritically accepts the work of Sheldon on constitution and temperament—which Hanhart, many pages later in the same book, does not. Sorsby's account of genetic disorders of the eye is most enlightening, and two pedigrees are given of what appear to be mutations. Lindenov discusses the genetics of disorders of "The ear," and Rushton writes on "The teeth." Here it could have been wished that the coverage had been a little fuller. Rushton unaccountably omits many of the fundamental references to the literature. Carter on the "Alimentary system" is most interesting, but one could wish that he had discussed the embryogenetics of cleft-palate and hare lip somewhat more in detail. Lindenov discusses the "Respiratory organs" and Herndon the "Cardiovascular system." Neel ably covers the field of "Inherited abnormalities of the cellular constituents of the blood," and Jackson briefly but adequately sets out the facts about "The haemorrhagic diatheses"—mainly hemophilia. Stratton's account under "Serology," of the blood groups and types is exemplary. Tage Kemp on "The urogenital system" and Bartels on "Endocrine disorders" are most informative, and so is Hanhart on "Infectious diseases" and Schwartz on "Allergy." Gorer concludes the book with a splendid chapter on "Cancer."

There is a good selected bibliography and an index.

Altogether this is a notable contribution surveying our knowledge of clinical genetics to date.

ASHLEY MONTAGU

## BOOKS RECEIVED

- THE ATOM STORY. By J. G. Feinberg. 243 pp. Philosophical Library, New York. 1953. \$4.75.
- ADJUSTMENT TO PHYSICAL HANDICAP AND ILLNESS: A SURVEY OF THE SOCIAL PSYCHOLOGY OF PHYSIQUE AND DISABILITY. By Roger G. Barker. xvi + 440 pp. Social Science Research Council, New York. 1953. \$2.00.
- VARIATIONS IN HUMAN BODY-BUILD, a Somatometric and X-Ray cephalometric Investigation on Scandinavian Adults. By Bengt Lindegard. 163 pp. Berlingska Boktryckeriet, Lund, Sweden. 1953.
- SYMPOSIUM ON FATIGUE. Edited by W. F. Floyd and A. T. Welford. viii + 196 pp. H. K. Lewis and Co., Ltd., London, 1953. \$4.00.
- THE MEANING OF SOCIAL MEDICINE. By Iago Galdston. viii + 137 pp. Harvard University Press, Cambridge, Massachusetts. 1954. \$2.75.
- FIFTY YEARS OF MEDICINE. By Lord Horder. 70 pp. Philosophical Library, New York. 1954. \$2.50.
- THE FIRST AUSTRALIANS. By Ronald M. Berndt and Catherine H. Berndt. 144 pp. Philosophical Library, New York. 1954. \$4.75.
- A DEVOTION TO NUTRITION. By Frederick Hoelzel. 88 pp. Vantage Press, Inc., New York. 1954. \$2.50.
- THE HUMAN ANIMAL. By Weston LaBarre. xv + 372 pp. The University of Chicago Press, Chicago, Illinois. 1954. \$6.00.
- SYMPOSIUM ON HUMAN FACTORS IN EQUIPMENT DESIGN. Edited by W. F. Floyd and A. T. Welford. viii + 132 pp. H. K. Lewis and Co., Ltd., London. 1954. \$4.00.
- A METHODOLOGICAL, PSYCHIATRIC AND STATISTICAL STUDY OF A LARGE SWEDISH RURAL POPULATION. By Tage Larsson and Torsten Sjögren. 250 pp. Acta psychiat. neurol. Scandinav., Supplementum 89, Copenhagen. 1954.
- BEYOND THE GERM THEORY. By Iago Galdston. viii + 182 pp. Health Education Council, New York. 1954. \$4.00.
- PSYCHOMOTOR ASPECTS OF MENTAL DISEASE. By H. E. King. xiv + 185 pp. Harvard University Press, Cambridge, Massachusetts. 1954. \$3.50.
- THE RACIAL AFFINITIES OF THE BAGANDA AND OTHER BANTU TRIBES OF BRITISH EAST AFRICA. By Lawrence Oschinsky. x + 188 pp. W. Heffer and Sons, Ltd., Cambridge, England. 1954. 25 S.
- THE DEAF AND THEIR PROBLEMS. By Kenneth W. Hodgson. xx + 364 pp. Philosophical Library, New York. 1954. \$6.00.
- CHILD PSYCHOLOGY. By Arthur T. Jersild. xii + 676 pp. Prentice Hall, New York. 4th ed., 1954. \$8.00.
- SOCIAL SCIENCE IN MEDICINE. By Leo W. Simmons and Harold G. Wolff. 254 pp. Russell Sage Foundation, New York. 1954. \$3.50.
- SYMPOSIUM ON PROBLEMS OF GERONTOLOGY. Edited by Robert S. Goodhart. ii + 141 pp. Nutrition Symposium Series, Number 9, National Vitamin Foundation, Inc., New York. 1954. \$2.50.

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